Computational and brain stimulation approaches to study the influence of visually guided comparisons in value-based decision-making

Dissertation
submitted to the
Faculty of Business, Economics and Informatics
of the University of Zurich

to obtain the degree of
Doktor der Neuroökonomie, Dr. sc.
(corresponds to Doctor of Neuroeconomics, PhD)

presented by

Manuel Andres Mitsumasu Heredia
from Peru

Approved in October 2017 at the request of
Prof. Dr. Ernst Fehr
Prof. Dr. Todd Hare

The Faculty of Business, Economics and Informatics of the University of Zurich hereby authorizes the printing of this dissertation, without indicating an opinion of the views expressed in the work.

Zurich, 25.10.2017

Chairman of the Doctoral Board: Prof. Dr. Todd Hare

Acknowledgments

First, I would like to thank my advisor, Ernst Fehr, who gave me the opportunity to do this thesis.
I also feel very thankful to Todd Hare, the second supervisor of this thesis, and Ian Krajbich. Thank you both for your valuable advice in these projects.
Moreover, I want to thank Christian Ruff for his suggestions and advice on the experimental design of two studies presented here.
Further thanks to my collaborators in these projects, Gaia Lombardi and Rafael Polania.
Finally, I want to thank my family, my friends and Rahel for their ongoing support and encouragement.

Abstract

Value-based decision-making occurs whenever an organism makes a choice on the basis of its subjective preferences. While value-based decisions have been traditionally regarded as a simple maximization problem, recent investigations suggest that cognitive functions such as visual attention have an impact on decision processes and, therefore, can drive choices. These reports have shown strong correlations between eye movements and choice behavior, and suggest that visual comparisons of the available alternatives influence preferences.

However, despite the increasing evidence on the relationship between visual comparisons and choices, the issue of causality has remained unclear. In particular, it is unclear whether modulations of neuronal activity in attention-related brain regions induce changes in choice behavior. By combining brain stimulation and computational techniques, I investigate the causal role of visual comparisons on value-based decision-making. A first study explores the role of the posterior parietal cortex (PPC) – a brain region involved in both visual attention and value-based decision-making – during simple value-based decisions. Our results indicate that inter-hemispheric transcranial direct current stimulation (tDCS) on the PPC induce spatial biases in visual comparison processes, which in turn, lead to spatial biases on choice. A second study examines the role of the right Frontal Eye Field (FEF) - a brain area that is mainly involved in attentional processes - in simple value-based choices. This study shows that inhibitory transcranial magnetic stimulation (TMS) on the right FEF reduces the influence of visual comparisons in the decision process.

Traditional views on decision-making have been also challenged by empirical data showing that preferences can be context-dependent. For example, decision-makers tend to prefer a sure option to a risky prospect when the alternatives are presented as gains, even when both options have the same expected value. However, if options are presented as losses this aversion to risk is reduced, even though options remain the same in terms of outcomes. In a third study, we examine which is the role of visual comparisons in frame-depended preferences. This study shows that

contextual information about the available options can lead the decision-maker to engage more in visual comparison processes. This increased influence of visual comparisons on the decision process, in turn, modulates the decision-maker's choice tendency.

List of manuscripts

The dissertation is based on the following research articles[1]:

Study 1:

Mitsumasu. A., Krajbich. I., Polania. R., Fehr. E., Ruff. C. Value comparisons during economic choice are causally linked to interhemispheric balance in the parietal cortex. *In preparation.*

Study 2:

Mitsumasu. A., Krajbich. I., Polania. R., Ruff. C., Fehr. E. Stimulation of the right frontal eye field modulates the dynamic effects of attention on choice. *In preparation.*

Study 3:

Mitsumasu. A., Lombardi. G., Fehr. E. Visual comparisons mediate context-dependent changes in preferences. *In preparation.*

[1] At the time of submission of my dissertation the articles corresponding to Study 2 and Study 3 are in preparation for submission to journals that could potentially exclude scientific work that is already published online. For that reason, these articles will be blocked from online publication in the central library and will only be accessible after one year.

Contents

General introduction

The capacity to make decisions and implement goal-directed actions is central to humans, animals and, more recently, non-biological organisms. This is a reason why the study of decision-making is in the interest of many disciplines, including economics, neuroscience, psychology, computer science and statistics.

Generally speaking, there are two types of decisions: Perceptual decisions, determined by objective states of the physical world, and value-based decisions, which are based on the subjective preferences of the decision-maker. Preferential choices have been a central topic in economics and normative theories in this field assume that individuals are consistent across their decisions (Von Neumann and Morgenstern, 1947). However, this assumption has been challenged by empirical evidence showing that choices can be influenced by contextual information (Kahneman and Tversky, 1984; Kahneman Tversky, A., 1979; McNeil et al., 1982; Tversky and Kahneman, 1981). In addition to these data, recent investigations suggest that they can also be influenced by visual comparisons of available options (Ashby et al., 2016; Cavanagh et al., 2014; Konovalov and Krajbich, 2016; Kovach et al., 2014; Krajbich and Rangel, 2011; Krajbich et al., 2010; Lim et al., 2011; Schonberg et al., 2014; Shimojo et al., 2003; Stewart et al., 2016; Towal et al., 2013; Vaidya and Fellows, 2015)..

In this dissertation I present three studies that investigate the computational and neural mechanisms related to visually guided comparisons in value-based decision-making (see appendix). Study 1 explores the role of the posterior parietal cortex (PPC) – a brain region involved in both the representation of value and attentional processes. Study 2 examines the role of the right Frontal Eye Field (FEF) – a cortical area involved, mainly, in visual attention. Study 3 examines the link between visual comparisons and context-dependent decisions.

In the introductory chapter, I summarize the theoretical framework of evidence-accumulation - which has guided these three studies - as well as findings on its neurobiological basis. Then, I give an overview of recent findings on the relationship between visual comparisons and value-based choice. The three studies will be summarized in the second chapter. Finally, a general discussion and conclusion form the third chapter.

Decision-making and evidence accumulation

While preferential choices have been traditionally studied in economics, investigations in neuroscience and psychophysics have approached decision-making with experimental studies on perceptual choices. These investigations have generally focused on both choice outcomes and decision speed, when individuals have to classify noisy sensory information. Because of this approach, these studies have repeatedly shown that individuals do not implement choices instantaneously, but the time required to take action varies according to the quality of the sensory stimulation (Bogacz et al., 2010; Chittka et al., 2009; Schouten and Bekker, 1967; Wickelgren, 1977). Simply put, this documentation suggest that, in order to be accurate, decision-makers have to invest more time when facing ambiguous sensory input. On the contrary, when facing sensory input with low uncertainty decision-makers tend to be faster. This need to invest time in order to achieve a certain level of perceptual accuracy – also named “speed-accuracy trade-off” – has led researcher to believe that decision-makers gradually accumulate sensory information in time until the accumulated perceptual input provides enough evidence in favor of one alternative of the decision problem.

In order to formally capture this dynamical decision process, many mathematical models - known as “sequential sampling models” - have been proposed (Busemeyer and Townsend, 1993; Laming, 1968; Ratcliff and McKoon, 2008; Roe et al., 2001; Usher and McClelland, 2001; Vickers, 1970). The common trait of all these models is that they characterize the evidence accumulation process as a decision variable that evolves stochastically in time until it reaches a threshold corresponding to one option (Bogacz, 2007; Bogacz et al., 2006; Deco et al., 2013; Mulder et al., 2014; Zhang et al., 2009).

The concept of evidence accumulation has become appealing because its mathematical formulations allow researcher to decompose decision processes in order to identify latent cognitive mechanisms underlying behavioral observations (de Gee et al., 2017; Mulder et al., 2012, 2014). In addition to this methodological advantage, findings in humans and non-humans primates have shown patterns of neuronal activity that might support accumulation processes. For instance, during a visual motion direction discrimination task, neurons in the lateral intraparietal (LIP) cortex of macaque monkeys exhibit a gradual increase in their firing rate. When facing very ambiguous motion stimuli, subjects are slower and LIP neuronal activity increases at a slow rate. On the contrary, when the visual information is clear, subjects are faster and LIP neurons activity increases at a fast rate. Furthermore, independently of the level of difficulty, LIP neurons reached the same level of activation when subjects initiated their response. Similar to sequential sampling models, these patterns of neuronal activity mimic evidence accumulation process with a boundary-crossing criterion (Gold and Shadlen, 2007; Roitman and Shadlen, 2002; Shadlen and Kiani, 2013). In line with these results, another study has shown that electrophysiological signals from the human parietal cortex reflect accumulation-related brain activity during perceptual decisions (O'Connell et al., 2012).

Recently, value-based decision-making has become an important topic in the field of neuroscience, and a central goal in this line of research is to understand which are the cognitive, computational and neurobiological mechanisms that allow decision-makers to implement this type of choices (Rangel et al., 2008). Several of these investigations have studied value-based choices with the conceptual and formal framework of evidence accumulation (Basten et al., 2010; Cavanagh et al., 2011; Hare et al., 2011; Hunt et al., 2012; Krajbich and Rangel, 2011; Krajbich et al., 2010, 2015; De Martino et al., 2012; Philiastides and Ratcliff, 2013; Polanía et al., 2014; Roe et al., 2001; Tajima et al., 2016; Towal et al., 2013). Here, it is important to precise that a general assumption of accumulation models for value-based decisions is that evidence is not provided by one stream of noisy sensory information, but by the subjective values that the decision-maker assign to each option.

One of these studies, for instance, has combined functional magnetic resonance imaging (fMRI) with a neurally adapted evidence accumulation model in order to identify brain networks involved in value-based decision-process. The authors found a correlation between activity in the ventromedial prefrontal cortex (vmPFC) and the subjective values of available options. Furthemore, the neurally adapted accumulation model predicted activity in the dorsomedial prefrontal cortex (dlPFC) and intraparietal sulcus (IPS), which suggest a relationship between this areas and the process of comparing option values. This view is also supported by further functional connectivity analyses, which revealed an enhanced coupling between these areas and motor regions in charge of implementing the choice (Hare et al., 2011).

Another investigation has shown that evidence accumulation processes for value-based decisions are, nonetheless, distinguishable from those of perceptual decisions at the neural level. In this study, subjects perform a perceptual and a value-based task with same visual stimuli. Therefore, it was possible for the authors to compare within-subjects behavioral and neuronal patterns from both tasks. Results from this study showed that, in both type of choices, oscillations at the gamma band correlated with evidence accumulation processes predicted by a sequential sampling model. Importantly, these accumulation-related gamma oscillations were also observed in frontal regions, but only during value-based choices. Additionally, fronto-parietal synchronization was stronger in value-based decision (Polanía et al., 2014). According to the authors, these results indicate that an additional process is performed in value-based decisions. The implementation of subjective value signals might be this process.

Decision-making and visually guided comparisons

In order to choose, a decision-maker has to compare the available options. This statement raises an important question: Which are the mechanisms that allow decision-makers to compare available alternatives? There has been an increasing interest in this question and recent studies have particularly focused in the role of attention-related processes during value-based choice.

Several studies have shown strong correlations between choice and gaze patterns (Ashby et al., 2016; Cavanagh et al., 2014; Konovalov and Krajbich, 2016; Kovach et al., 2014; Krajbich and Rangel, 2011; Krajbich et al., 2010; Lim et al., 2011; Schonberg et al., 2014; Shimojo et al., 2003;

Stewart et al., 2016; Towal et al., 2013; Vaidya and Fellows, 2015). More precisely, these reports have shown that, in decisions involving attractive options, more gaze/dwell time is allocated on the chosen alternative compared to the others.

The relationship between gaze and choices has been mathematically characterized with a Drift Diffusion Model (DDM) that assumes an influence of attentional process in accumulation of evidence. The main difference between this attentional DDM (aDDM) and traditional sequential sampling models is that the aDDM incorporates a parameter that discounts the unattended option value and, thus, bias the decision process in favor of the attended one (Krajbich and Rangel, 2011; Krajbich et al., 2010).

In addition to this report, other investigations obtain empirical evidence for the influence of visual comparisons in decision-making. These studies have tried to influence choice behavior by manipulating the amount gaze/dwell time that subjects spend on each option. One of those studies showed that control of gaze/dwell time had indeed differential effects - however small – in choice behavior. When decision makers had to choose between attractive options, increasing the gaze/dwell time of one alternative (from 300 to 900 ms) led to a higher likelihood of choosing that option (7%) (Armel et al., 2008). An fMRI study used a similar task and showed effects of similar sizes. One important distinction is that this study examined the effect of gaze across many difficulty levels (hard decision involving options with very similar values and easy decisions involving options with very different values) and showed that gaze/dwell time control mainly affected hard decisions. The imaging data from this study showed that activity in the vmPFC and ventral striatum (vStr) correlated with the difference in value between the attended and the unattended items (Lim et al., 2011). A particular limitation in these two experiments is that the manipulation of gaze allocation does not imply a manipulation of attentional processes during choice. In natural conditions, visual attention and gaze are closely coupled. However, when eye movements are constrained, the orienting and control of visual attention can be deployed covertly (Carrasco, 2011).

Nonetheless, a recent study has shown that patients with damage on dorsomedia prefrontal cortex (dmPFC) exhibit an exaggerated influence of visual comparisons on choice, while patients with damage on vmPFC do not show this bias. These findings suggest that the dmPFC, is causally involved in controlling the relative influence of visual comparisons in decision-making (Vaidya and Fellows, 2015).

Finally, a recent study has provided, for the first time, evidence for cellular-level mechanisms at the basis of attention-guided value-based choices (McGinty et al., 2016). Previous neurophysiological investigations in non-human primates have shown that the values of offered and chosen options are correlated with the activity of some neurons in the orbitofrontal cortex (OFC) (Padoa-Schioppa and Assad, 2008, 2006). In light of these results, researchers in this recent study examined the response of OFC neurons to value-associated visual cues, when macaques performed a free viewing task. Their results show that a majority of OFC neurons encoded the distance between the overtly attended area of the screen and the cue, but when this distance was short, activity in some of OFC neurons was modulated by associated value of the cue.

Overview of the studies

Study 1: tDCS on the PPC bias visual comparisons and choices

Background

Recent investigations suggest that, during value-based decisions, visual comparisons of the available options temporarily bias the decision process in favor of the attended alternative and, therefore, guide preferences (Krajbich and Rangel, 2011; Krajbich et al., 2010). While these and other reports (Ashby et al., 2016; Cavanagh et al., 2014; Konovalov and Krajbich, 2016; Kovach et al., 2014; Lim et al., 2011; Schonberg et al., 2014; Shimojo et al., 2003; Stewart et al., 2016; Towal et al., 2013; Vaidya and Fellows, 2015) have shown strong correlations between gaze patterns and choice behavior, it is still unclear whether it is possible to modulate the neural mechanisms at the basis of this visually guided decision process in order to influence choice.

The PPC is a brain area involved in both, decision-making processes (Filimon et al., 2013; Hare et al., 2011; Heekeren et al., 2004; Platt and Glimcher, 1999; Polanía et al., 2014; Roitman and Shadlen, 2002; Sugrue et al., 2004) and the allocation of visual attention (Corbetta et al., 2005; Giglia et al., 2011; Hilgetag et al., 2001; Kinsbourne, 1977; Nyffeler et al., 2008; Sparing et al., 2009; Vuilleumier, 2013; Vuilleumier et al., 1996). Therefore, this region might be involved in attentional modulation of choice. In this study we explored how modulations of neuronal activity in the PPC, by means of tDCS, alter choice behavior. Based on previous findings on the PPC, we tested two competing hypotheses about the effects of stimulation. On the one hand, previous studies have shown that lesions and inhibitory stimulation of the right PPC induce attentional biases towards the right side of the visual scene. Interestingly, in the case of tDCS, it has been reported that bi-hemispheric Left anodal/Right cathodal stimulation on the PPC (LA-RC) leads to stronger effects than inhibitory unilateral stimulation (i.e. only cathodal stimulation on the right PPC) (Giglia et al., 2011; Hilgetag et al., 2001; Nyffeler et al., 2008; Sparing et al., 2009). Thus, according to our first hypothesis, LA-RC tDCS on the PPC would induce an attentional bias towards alternatives presented on the right side of the visual display. This attentional bias would, in turn, increase the tendency to choose these options. On the other hand, studies in decision-making indicate that the PPC is also involved in the representation of value (Kahnt et al., 2014; Platt and Glimcher, 1999; Polanía et al., 2014) and evidence-accumulation processes underlying choice (Heekeren et al., 2004; O'Connell et al., 2012; Roitman and Shadlen, 2002). Based on these reports, our second hypothesis stipulates that bilateral tDCS on the PPC would alter the contribution of attended and unattended options during the decision process.

Methods

Forty human subjects (16 females) participated in the experiment. In a first task, subjects rated 148 food items. This rating task gave us a measure of the subjective value for each food item and allowed us to exclude disliked items. In a second task, participants made 195 decisions between pairs of positively rated food items. Subjects performed the choice task while receiving bi-hemispheric tDCS over the posterior parietal cortex (PPC). One group of subjects (n = 14) received left cathodal–right anodal stimulation (LC-RA), a second group (n = 13) received left anodal–right cathodal stimulation (LA-RC), and a third group received Sham stimulation (n = 13).

In each trial, one of the food items was presented on the left and the other on the right side of the screen. Decisions were self-paced and were made using the computer keyboard. The food items we presented in the choice task were selected such that – for each participant – the difference in ratings between the left and right items (VD = left item value - right item value) was constrained to be -1, 0 or +1, with an equal number of trials (65) of each. This was done to focus on difficult choice problems where tDCS-induced changes in the decision process would be more likely to change the choice outcomes. Subjects knew that at the end of the experiment, one trial would be selected at random and that they had to eat the food item that they chose in that trial (see Materials and Methods section in Appendix A).

To test our two alternative hypotheses, we analyzed possible stimulation effects on subjects' choice behavior. We ran a logistic mixed-effects regression of the likelihood of choosing the left food item as the dependent variable, with value difference (VD = left item value – right item value), overall value (OV = left item value + right item value) and stimulation group dummies as independent variables. We also included interactions of OV and VD with the stimulation group dummies and random effects to account for repeated within-subject measures. Then we analyzed subjects' reaction times (RTs) with an analogous linear mixed-effects regression. Finally, we ran a third mixed-effects logistic regression to further identify any effects of tDCS on choice consistency (i.e., the likelihood of choosing the item with the higher rating). We only included choices between unequally rated items (VD $\neq$ 0) in this analysis (See Supplementary material of Appendix A).

To test how the effects of the different tDCS montages could best be explained, we simulated an attentional version of a Drift-Diffusion Model (aDDM) (See Materials and Methods section). This theoretical framework allowed us to decompose the decision process and estimate which of its aspects was modulated by stimulation.

Results and conclusion

In our first analysis, we could not observe a main effect from LA-RC or LC-RA tDCS on choices. However, relative to the baseline Sham group, subjects receiving LA-RC stimulation were more likely to choose the left item as the OV increased. Note that this choice bias in favor of the left option is opposite of the one predicted by the first hypothesis. Additionally, no interaction effect was observed between LC-RA stimulation and OV. Our analysis on RTs revealed that, in general, subjects were faster in decision with higher OV. Relative to the Sham group, this effect was stronger with LC-RA stimulation, but not with LA-RC stimulation. Finally, our analysis on choice consistency revealed that subjects receiving LC-RA stimulation were less consistent with their earlier ratings than subjects in the baseline Sham group. However, this effect was not observed with LA-RC stimulation.

These complex behavioral patterns provide evidence against our first hypothesis. Could our second hypothesis – which states that tDCS modulates the contribution of attended and unattended options during the decision process – explain them? To test this hypothesis, we used the aDDM to examine the simplest stimulation-induced parameter changes that can account for these behavioral patterns pattern. More precisely, we tested different parameterizations of the model that simulated symmetric tDCS-induced changes in the decision process. Only one of these models could replicate these behavioral patterns. This model is based on the idea that LA-RC stimulation induces a stronger discount on the value of the unattended option at the right side of the visual scene, while LC-RA leads to a stronger discount of the alternative at the left side when unattended. These results support the idea that bilateral tDCS over the PPC causes a symmetric spatial bias in the integration of value, resulting in biased choices.

Study 2: Inhibitory TMS on the right FEF reduces the influence of visual comparisons on choice

Background

It is widely agreed that an important function of visual attention is to allocate greater computational resources to elements of interest in the visual scene, at the cost of diminishing the processing of unattended components (Carrasco, 2011; Chelazzi et al., 2011; Itti and Koch, 2001). In line with this view, recent investigations suggest that, when facing different rewards, a decision-maker engages in visually guided comparisons that bias the decision process in favor of the attended alternative (Krajbich and Rangel, 2011; Krajbich et al., 2010). However it is not clear whether modulations of neuronal activity at the basis of visual attention processes lead to changes in choice behavior.

The control of visual attention is based on a large brain network (Chelazzi et al., 2011; Corbetta and Shulman, 2002; Gilbert and Li, 2013; Squire et al., 2013). However, large amount of evidence in both humans (Corbetta et al., 2002; Grosbras and Paus, 2002; Ruff et al., 2006; Saygin and Sereno, 2008; Serences et al., 2005; Silvanto et al., 2006) and non-human primates (Ekstrom et al., 2008; Moore and Armstrong, 2003; Moore et al., 2003; Thompson et al., 1997, 2005) have repeatedly confirmed the crucial role of the FEF on the selective allocation of attention. Additionally, unlike the PPC, this cortical area has not been related to the representation of value.

Combining TMS, eye tracking and computational modeling techniques, we conducted a study to test whether neural computations in the right FEF guide value-based decisions.

Methods

Forty-five subjects (20 females) participated in the experiment. In a first task, subjects rated 148 food items. This rating task gave us a measure of their subjective value for each food item and allowed us to exclude disliked items. After the rating task, subjects received inhibitory continuous theta burst TMS (Huang et al., 2005) over the right FEF (n = 23) or control stimulation on the vertex (n = 22). Right after stimulation subjects performed a self-paced binary choice task (180 decisions) between pairs of positively rated food items. The food items we presented were selected such that – for each participant – the difference in ratings between the left and right items (VD = left item value - right item value) was constrained to be -1, 0 or +1. As mentioned before, this was done to focus on difficult choice problems where attention is more likely to change the choice outcomes. Additionally, this task had two conditions. In the high OV condition, subjects had to choose between two very appetitive (highly rated) foods, whereas decisions in the low OV condition only involved slightly appetitive (low rated) options. During this task, subjects gaze patterns were recorded with an eye tracker.

We ran a logistic mixed-effects regression in which the choice of the longer attended food item was the dependent variable, with a dummy variable for FEF-TMS group, the dwell time advantage and the OV condition as fixed effects, and all their interactions. We also used random effects for repeated measures within subjects. Subjects' decision speed was analyzed with a linear mixed-effects regression of RTs, with stimulation group, OV condition and their interaction as fixed effects, and random effects for repeated measures within subjects (see Supplementary Tables 3 and 4 for a detailed description of the regression results).

Finally, we fitted the aDDM to the individual data of each participant with maximum likelihood estimations (MLE) in order to examine which aspect of the decision process was modulated by FEF-TMS.

Results and conclusions

With regard to choices and RTs, we tested specific hypotheses based on the aDDM. The aDDM predicts that subjects in the Vertex group should be inclined to select the longest attended alternative and, during high OV decisions, this choice tendency should be stronger and coupled with faster responses. We confirmed that, indeed, during low OV decisions, subjects were more inclined to choose a food item as its dwell-time advantage (relative to the other option) increased. Additionally, this choice tendency in favor of the longest attended item was enhanced during high OV decisions and coupled with shorter RTs.

We also hypothesized that inhibitory TMS on the right FEF would decrease the influence of visual comparisons in the decision process. According to our computational model, this stimulation effect would lead to a reduced choice tendency in favor of the longest attended item and longer RTs in comparison to the Vertex group. Importantly, the aDDM implies that FEF-TMS should particularly affect choices and decision speed during high OV decisions. This was also corroborated by our results. During high OV decisions, subjects who received inhibitory TMS over the FEF were less likely to choose the longest attended food item and displayed a greater proportion of slow responses than the control group.

When comparing the parameters of subjects in both groups, we observed that participants in the FEF-TMS group had in general a weaker attentional discount than participants in the control group. Furthermore, we could not observe difference between stimulation groups, with respect of the other parameters. Taking together these effects show that inhibitory TMS on the right FEF modulates the influence of visual comparisons in decision-making.

Study 3: Visual comparisons and context-depended preferences

Background

Standard economic theory assumes that choices can be represented as a simple maximization process, and therefore preferences should be context-independent (Von Neumann and Morgenstern, 1947). However, empirical data has challenged this view by showing that contextual information influences preferences. For instance, Kahneman and Tversky have shown that humans tend to prefer sure options over risky prospects when alternatives are presented as gains, but this aversion to risk if diminished if the alternatives are presented as losses - even though both decision problems are identical in terms of possible outcomes (Kahneman and Tversky, 1984; Kahneman Tversky, A., 1979).

While context-dependent choices have been largely documented in humans and other species (Lea and Ryan, 2015; Louie et al., 2013; Shafir et al., 2002), we still know relatively little about the cognitive or computational mechanisms that drives them. In this study, we examine the influence of value comparisons in choice biases related to loss and gain frames during risky decision problems.

Methods

Thirty subjects (12 females) participate in our experiment. They were asked to make a series of binary decisions (140) between a risky option (a gamble) and a sure alternative (a safe option) that had the same expected value (EV). Each trial started with an initial monetary endowment. Additionally, the safe option was framed as a gain in one condition or as a loss in another condition. Thus, this experimental design allowed us to test the effect of framing within subjects. During the choice task, we also recorded subjects' gaze patterns.

To analyze subjects choices, we conducted a logistic mixed-effects regression in which the choice of the safe option was the dependent variable, with a dummy variable for Frame condition, the percentage of dwell time on the safe option and its EV as fixed effects, together with all their interactions. We used random effects for repeated measures within subjects. Subjects' RTs were analyzed by means of a linear mixed-effects regression, with Frame condition and EV as fixed effects, together with all their interactions. We also used random effects for repeated measures within subjects.

In order to assess the role of visual comparisons in the observed choices, we also tested the predictive performance of two dynamical computational models. As the aDDM, our first model characterizes the decision as an evidence accumulation process guided by visual comparisons. On the contrary, our alternative model assumes that accumulation of evidence is independent of gaze patterns. We fitted both models to the individual data of each subject, separately for the Gain frame condition and the Loss frame condition. This fitting procedure allowed us to estimate parametric changes across framing conditions and, thus, determine whether changes in visual comparison processes where linked to changes in preferences (See the Introduction section of appendix 1 for a detailed description of the models).

Results and conclusions

We observed that subjects had a strong tendency to choose the safe option and this tendency was stronger as the EV of the options increased. However, in the Loss frame conditions this tendency was weaker. This indicates that, in general, choices were influenced by the contextual information of the safe option's frame. Importantly, we also observed strong relationships between choices and gaze patterns. The tendency to choose the safe option was stronger as the total gaze/dwell time allocated on this alternative increased. Additionally, this effect was enhanced when subjects faced options with higher EV. Finally, we observed that when the safe option had a higher gaze/dwell time advantage, the influence of the Loss frame in choices was weaker. With respect of RTs, we observed that subjects were faster when facing options with higher EV but, compared to the Gain frame condition, this effect decreased in the loss frame condition.

Following analyses examined how well our two competing theoretical frameworks replicated these behavioral patterns. These analyses revealed that the attentional accumulator model characterized choices with greater accuracy than the alternative model. This result indicates that visual comparisons played a role in these decisions.

Following analyses on the parameterizations of the attention accumulator model showed that, according to this model, subjects give a greater weight to the safe option (compared to the weight of the gamble) in both the Gain frame and the Loss frame condition. These analyses also revealed that the parameter capturing the attentional influence on choice (the parameter discounting the EV of the unattended option) was significantly affected by framing. In other words, parameter estimations of this model suggest that, in the Loss frame condition, the discount of the unattended option is stronger than in the Gain frame condition. These frame-dependent modulations were not observed in any other parameter of this model. Thus, the attentional accumulator model explains the observed choice patterns as follows: First, the decision process starts with an initial bias, which leads to the tendency to choose the safe option. Second, despite this initial bias in the decision process, evidence accumulation does not progress continuously on its advantage, but can change in favor of the gamble when attended. Third, a stronger influence of visual comparisons during the Loss frame condition further decreases the safe option's advantage on evidence accumulation, and therefore, weakens the tendency to choose this alternative. Analogous analyses showed that the alternative model was not able to capture framing-dependent changes in preferences with framing-dependent changes in specific aspects of the decision process.

Our attentional accumulator model explains within-subjects frame-dependent changes in choices, but also between-subjects differences with respect of the susceptibility to framing. Additional analyses showed that subjects with stronger frame-dependent modulations of the attentional discount experienced a stronger influence of frame in their choices.

To summarize, our results indicate that, in response to the presentation of available options, individuals modulate their investment in visual comparisons. These frame-dependent modulations of visual comparisons, in turn, lead to frame-dependent choices. Furthermore, our results also show that attention-related components of decision processes also explain why some decision-makers are more influenced by the presentation of options than others.

General discussion

Study 1

The first study tests two hypotheses on how tDCS over the PPC affects simple value-based choices. On the one hand, the first hypothesis was specific to one tDCS montage and stipulates that that LA-RC stimulation induces a bias in attentional focus towards the option at the right side of the visual scene that, in turn, would increase the likelihood of choosing this option. On the other hand, the second hypothesis suggests that bi-hemispheric tDCS over the PPC modulates the contribution of attended and unattended options in the decision process.

Data from our experiment showed a complex behavioral pattern. However, the observed behavior refuted the first hypothesis because, as the OV of the decision increased, subjects receiving LA-RC tDCS were more likely to choose the food item at the left side of the screen than subjects in the control group. To examine if this complex behavioral patterns could be explained by the second hypothesis, we simulated the aDDM with symmetric tDCS-induced changes in its parameters. Only a model based on the idea that LA-RC and LC-RA tDCS produces symmetric changes in the discount of unattended options could capture these behavioral patterns. These results suggest that our bilateral montage of LA-RC (LC-RA) increases the discount in the evidence accumulation process for an unattended right (left) option but has no effect on the discount factor for an unattended left (right) option.

It is important to note that we tested a restricted space of models, because our goal was to find the most parsimonious explanation for the observed behavioral effects. Nonetheless, with this procedure we were able to obtain a unifying explanation of the observed behavioral patterns.

Additionally, our simulations were based on gaze patterns obtained in a previous report (Krajbich et al., 2010) and, thus, our modeling exercise is based on the assumption that active tDCS montages did no alter gaze patterns. While the observed data rejected the first hypothesis (which implies an effect of LA-RC stimulation on the gaze allocation), future investigations should include analyses of gaze patterns in order to further assess the effects that tDCS over the PPC has on choice behavior.

An important question is how tDCS affects interconnected areas during value-based decisions. Previous investigations support the idea that synchronized fronto-parietal activity is a neural fingerprint of value-based choices (Hunt et al., 2012; Polanía et al., 2014, Siegel et al. 2008) and it is possible that the effects of our tDCS montages involve a reduced sensitivity of parietal areas for signals originating in the frontal cortex (Polania et al, 2015). Additionally, several investigations suggest that causal manipulations of neural activity parietal, frontal and collicular regions lead to asymmetric inter-hemispheric interaction and, therefore, biases in motor and perceptual functions (Filmer et al., 2015; Funk and Pettigrew, 2003; Giglia et al., 2011; Hummel and Cohen, 2006; Kobayashi et al., 2004; Lefebvre et al., 2012; Sparing et al., 2009; Takeuchi et al., 2009; Weddell, 2004; Wright and Krekelberg, 2014). Our study provides suggestive evidence for the role of these inter-hemispheric dynamics in value-based choice and motivates further research into the precise underlying mechanisms.

To summarize, we combined tDCS and computational modeling techniques to demonstrate that value-based choices can be manipulated by stimulating PPC. Our results support the idea that bilateral tDCS over the PPC modulates the contribution of attended and unattended options, resulting in spatially biased choices.

Study 2

Based on the aDDM, we designed an experiment to test whether the right FEF is causally linked to value-based decisions. As predicted by our model, subjects receiving control stimulations were more likely to choose the longest attended option than the other alternative, and during high OV decision this choice tendency was stronger and coupled high shorter RTs. We also hypothesized that inhibitory TMS over the right FEF decreases the influence of visual comparisons in the decision-making process. According to our theoretical framework, this effect should then diminish the tendency to choose the longest attended option and increase RTs, but especially during decisions with high OV condition. We observed, indeed, that subjects in the FEF-TMS group were slower and less likely to choose the longest attended option than subjects in the control group, and these effects were specific to the high OV condition. Finally, for every subject we fitted the aDDM and results from parameter estimations support the idea that FEF-TMS modulated the influence of visually guided comparisons during the decision process.

In light of these results it is natural to ask which are the neuronal mechanism that allow visual attention to modulate value-based decision processes. Research in perceptual decision-making have shown that subjects have greater sensitivity (Barbot et al., 2011; Herrmann et al., 2010; Montagna et al., 2009; Pestilli and Carrasco, 2005; Pestilli et al., 2007) and stronger neuronal responses in the visual cortex (Connor et al., 1997; Kastner et al., 1998; Liu et al., 2005; Martinez-Trujillo and Treue, 2002; O'Craven et al., 1997; Reynolds and Desimone, 2003; Reynolds et al., 2000) for attended visual stimuli than unattended ones. Additionally, large evidence suggest that these attention-dependent behavioral effects and its neural correlates are linked to modulations of neuronal activity in the FEF (Gregoriou et al., 2009; Moore and Armstrong, 2003; Moore and Fallah, 2004; Ruff et al., 2006; Silvanto et al., 2006). It might be possible that visually guided comparisons of value rise from a similar mechanism. A recent investigation suggest that neuronal representations of value can be modulated by visual attention (Lim et al., 2011). Additionally, recent studies have revealed that fronto-parietal synchronization at the gamma frequency is a neuronal fingerprint of value-based decision processes and decreasing the degree of coherence between parietal and frontal activity leads to inaccurate choices (Polanía et al., 2014, 2015).

Taking together, our findings demonstrate the relevance of the right FEF for attention-dependent modulations of value-based decision processes, and, more generally, they suggest directions for future investigations on the interaction between visual-attention brain networks and areas exhibiting value-signals.

Study 3

Based on previous documentation on the influence of visual comparisons processes in decision-making, we conducted a study to explore the role of these processes in context-dependent preferences. Subjects showed a strong inclination to choose a safe option over a gamble when the sure alternative was framed as a gain, and this choice tendency was specially pronounced when the decision problem involved options with high EV. However, when the safe option was presented as a loss, the propensity to choose the safe option was reduced. This result confirmed that subjects' preferences were influenced by the contextual information provided by framing. Interestingly - in line with previous documentation (Ashby et al., 2016; Cavanagh et al., 2014; Kovach et al., 2014; Krajbich and Rangel, 2011; Krajbich et al., 2010; Lim et al., 2011; Schonberg et al., 2014; Shimojo et al., 2003; Stewart et al., 2016; Towal et al., 2013; Vaidya and Fellows, 2015) - we also observed that this choice tendency was stronger as the gaze/dwell time advantage of the safe option increased.

We then compared the predictive performance of two sequential sampling models on the observed choices. The first model characterizes the decisions as a process of evidence accumulation influenced by visually guided comparisons of the available options. On the contrary, the second model does not assume an influence of value comparisons. Results on model fits corroborated that the attentional accumulator model predicted choice behavior with greater accuracy than the alternative model.

According to the attentional accumulator model, subjects start the decision process with an initial bias in favor of the safe option but visual comparisons reduce the impact of this bias on choice behavior. Importantly, this model also suggests that subjects are generally more engaged in visual comparisons during Loss frame decisions (relative to Gain frame decisions), and therefore less driven by the initial bias of the decision process. Simply put, this model suggests that, compared to Gain frame decisions, subjects are further engaged in visual comparisons during Loss frame decisions. In addition, our model also captures between-subject variability in context-dependent choice behavior. More precisely, this model indicates that subjects who are strongly (weakly) engaged in visual comparisons show big (small) framing-dependent changes in preferences. According to recent research decision-makers who know in advance which option to select are less invested in a visual comparison process. On the contrary, when choices are not determine in advance, these comparisons can influence preferences (Konovalov and Krajbich, 2016). Our results are in line with this documentation.

A previous investigation has shown that the effect of framing on choices is correlated with modulations of neuronal activity in the amygdala (De Martino et al., 2006). According to the authors, these modulations might reflect shifts from predominantly “emotionally-based” preferences to more “analytic-based” choice behavior. In light of these results it is important to ask to which extend frame-induced changes in emotional states lead decision-makers to engage/disengage in visually guided comparisons. Further investigations are necessary to determine the link between emotional and attentional components of decision-making.

Previous investigations have examined context-dependent decisions by means of sequential sampling models (Bogacz et al., 2007; Tsetsos et al., 2010, 2012, 2016; Usher and McClelland, 2004). These reports suggest that different frames induce changes on how decision-makers weight the available options. However, a distinction of our study is that it provides for the first time evidence indicating that visually guided comparisons play a role in context dependent-preferences.

General conclusions

Most of the research on value-based decision-making and attentional processes has provided correlational data showing the strong coupling between gaze and choice patterns. The first two studies presented in this thesis (Study 1 and 2) show that it is possible to exogenously modulate the influence of visual comparisons in value-based decisions. Study 1 indicates that bi-hemispheric tDCS over the PPC can regulate the contribution of attended and unattended options in the decision-process. This effect, in turn, leads to spatially biased decision-processes. Results from Study 2 show that inhibitory TMS over the right FEF reduces the influence of visual comparisons in a spatial-independent manner.

Standard sequential sampling models include a stochastic component that allows them to replicate variability in choice behavior. An advantage of the aDDM is that it can explain variance in choices with an attentional mechanism, in addition noise. In Study 3, we used a slightly different version of the aDDM to examine the effect of visual comparisons in context-dependent decision processes. Results from this study indicate that, in response to contextual information, subjects regulate their engagement in visual comparisons during their decisions. Context-dependent changes in the influence of visual comparisons, in turn, lead to context-dependent choices

A key assumption of the aDDM (and the modified version in Study 3) is that, when comparing options, the value of the attended alternative is better integrated than the value of the unattended one. Interestingly, this is line with research on attention in the perceptual domain. These investigations suggest that a main function of selective attention is to filter perceptual input and enhance contrast sensitivity and spatial resolution in favor of the attended region of the visual scene(Barbot et al., 2011; Carrasco, 2011; Herrmann et al., 2010; Pestilli and Carrasco, 2005; Pestilli et al., 2007). The aDDM proposes a similar mechanism for the value processing. More precisely, this model suggests that decision makers allocate more computational resources for the processing of the attended option value.

This idea is also in line with certain views of “bounded rationality” in decision-making (Simon et al., 1955). According to this perspective, one intrinsic limitation of decision-makers is their limited capacity to process information the decision-problem, and this limitation is particularly disadvantageous when facing time constraints.

In conclusion, our findings indicate that the attention-related brain region such as the PPC and the right FEF are involved in the comparisons of values, and therefore, in preferential choices. Furthermore, these attentional components of decision-making are involved in context-dependent changes of preferences.

References

Armel, K.C., Beaumel, a., and Rangel, a. (2008). Biasing simple choices by manipulating relative visual attention. Judgm. Decis. Mak. *3*, 396–403.

Ashby, N.J.S., Jekel, M., Dickert, S., and Glöckner, A. (2016). Finding the right fit: A comparison of process assumptions underlying popular drift-diffusion models. J. Exp. Psychol. Learn. Mem. Cogn. *42*, 1982–1993.

Barbot, A., Landy, M.S., and Carrasco, M. (2011). Exogenous attention enhances 2nd-order contrast sensitivity. Vision Res. *51*, 1086–1098.

Basten, U., Biele, G., Heekeren, H.R., and Fiebach, C.J. (2010). How the brain integrates costs and benefits during decision making. Proc. Natl. Acad. Sci. U. S. A. *107*, 21767–21772.

Bogacz, R. (2007). Optimal decision-making theories: linking neurobiology with behaviour. Trends Cogn. Sci. *11*, 118–125.

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., and Cohen, J.D. (2006). The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. Psychol. Rev. *113*, 700–765.

Bogacz, R., Usher, M., Zhang, J., and McClelland, J.L. (2007). Extending a biologically inspired model of choice: multi-alternatives, nonlinearity and value-based multidimensional choice. Philos. Trans. R. Soc. Lond. B. Biol. Sci. *362*, 1655–1670.

Bogacz, R., Wagenmakers, E.-J., Forstmann, B.U., and Nieuwenhuis, S. (2010). The neural basis of the speed–accuracy tradeoff. Trends Neurosci. *33*, 10–16.

Busemeyer, J.R., and Townsend, J.T. (1993). Decision field theory: a dynamic-cognitive approach to decision making in an uncertain environment. Psychol. Rev.

Carrasco, M. (2011). Visual attention: The past 25 years. Vision Res. *51*, 1484–1525.

Cavanagh, J.F., Wiecki, T. V, Cohen, M.X., Figueroa, C.M., Samanta, J., Sherman, S.J., and Frank, M.J. (2011). Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold. Nat. Neurosci. *14*, 1462–1467.

Cavanagh, J.F., Wiecki, T. V, Kochar, A., and Frank, M.J. (2014). Eye tracking and pupillometry are indicators of dissociable latent decision processes. J. Exp. Psychol. Gen. *143*, 1476–1488.

Chelazzi, L., Della Libera, C., Sani, I., and Santandrea, E. (2011). Neural basis of visual selective attention. Wiley Interdiscip. Rev. Cogn. Sci. *2*, 392–407.

Chittka, L., Skorupski, P., and Raine, N.E. (2009). Speed-accuracy tradeoffs in animal decision making. Trends Ecol. Evol.

Connor, C.E., Preddie, D.C., Gallant, J.L., and Van Essen, D.C. (1997). Spatial attention effects in macaque area V4. J. Neurosci. *17*, 3201–3214.

Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. *3*, 201–215.

Corbetta, M., Kincade, J.M., and Shulman, G.L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. J. Cogn. Neurosci. *14*, 508–523.

Corbetta, M., Kincade, M.J., Lewis, C., Snyder, A.Z., and Sapir, A. (2005). Neural basis and recovery of spatial attention deficits in spatial neglect. Nat. Neurosci. *8*, 1603–1610.

Deco, G., Rolls, E.T., Albantakis, L., and Romo, R. (2013). Brain mechanisms for perceptual and reward-related decision-making. Prog. Neurobiol. *103*, 194–213.

Ekstrom, L.B., Roelfsema, P.R., Arsenault, J.T., Bonmassar, G., and Vanduffel, W. (2008). Bottom-up dependent gating of frontal signals in early visual cortex. Science *321*, 414–417.

Filimon, F., Philiastides, M.G., Nelson, J.D., Kloosterman, N. a, and Heekeren, H.R. (2013). How embodied is perceptual decision making? Evidence for separate processing of perceptual and motor decisions. J. Neurosci. *33*, 2121–2136.

Filmer, H.L., Dux, P.E., and Mattingley, J.B. (2015). Dissociable effects of anodal and cathodal tDCS reveal distinct functional roles for right parietal cortex in the detection of single and competing stimuli. Neuropsychologia 1–7.

Funk, A.P., and Pettigrew, J.D. (2003). Does interhemispheric competition mediate motion-induced blindness? A transcranial magnetic stimulation study. Perception *32*, 1325–1338.

de Gee, J.W., Colizoli, O., Kloosterman, N.A., Knapen, T., Nieuwenhuis, S., and Donner, T.H. (2017). Dynamic modulation of decision biases by brainstem arousal systems. Elife *6*, 1–36.

Giglia, G., Mattaliano, P., Puma, a, Rizzo, S., Fierro, B., and Brighina, F. (2011). Neglect-like effects induced by tDCS modulation of posterior parietal cortices in healthy subjects. Brain Stimul. *4*, 294–299.

Gilbert, C.D., and Li, W. (2013). Top-down influences on visual processing. Nat. Rev. Neurosci. *14*, 350–363.

Gold, J.I., and Shadlen, M.N. (2007). The neural basis of decision making. Annu. Rev. Neurosci. *30*, 535–574.

Gregoriou, G.G., Gotts, S.J., Zhou, H., and Desimone, R. (2009). High-Frequency, Long-Range Coupling Between Prefrontal and Visual Cortex During Attention. Science (80-.). *324*, 1207–1210.

Grosbras, M., and Paus, T. (2002). Transcranial magnetic stimulation of the human frontal eye field: effects on visual perception and attention. Eur. J. Neurosci. 1109–1120.

Hare, T. a., Schultz, W., Camerer, C.F., O'Doherty, J.P., and Rangel, a. (2011). Transformation of stimulus value signals into motor commands during simple choice. Proc. Natl. Acad. Sci. *108*, 18120–18125.

Heekeren, H.R., Marrett, S., Bandettini, P. a, and Ungerleider, L.G. (2004). A general mechanism for perceptual decision-making in the human brain. Nature *431*, 859–862.

Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., and Heeger, D.J. (2010). When size matters: attention affects performance by contrast or response gain. Nat. Neurosci. *13*, 1554–1559.

Hilgetag, C.C., Théoret, H., and Pascual-Leone, a (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced "virtual lesions" of human parietal cortex. Nat. Neurosci. *4*, 953–957.

Huang, Y.-Z., Edwards, M.J., Rounis, E., Bhatia, K.P., and Rothwell, J.C. (2005). Theta burst stimulation of the human motor cortex. Neuron *45*, 201–206.

Hummel, F.C., and Cohen, L.G. (2006). Non-invasive brain stimulation: a new strategy to improve neurorehabilitation after stroke? Lancet. Neurol. *5*, 708–712.

Hunt, L.T., Kolling, N., Soltani, A., Woolrich, M.W., Rushworth, M.F.S., and Behrens, T.E.J. (2012). Mechanisms underlying cortical activity during value-guided choice. Nat. Neurosci. *15*, 470–476, S1-3.

Itti, L., and Koch, C. (2001). Computational modelling of visual attention. Nat. Rev. Neurosci. *2*, 194–203.

Kahneman, D., and Tversky, A. (1984). Choices, values, and frames. Am. Psychol. *39*, 341–350.

Kahneman Tversky, A., D. (1979). Prospect theory: An analysis of decision under risk. Econometrica *47*, 263–291.

Kahnt, T., Park, S.Q., Haynes, J.-D., and Tobler, P.N. (2014). Disentangling neural representations of value and salience in the human brain. Proc. Natl. Acad. Sci. U. S. A. *111*, 5000–5005.

Kastner, S., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1998). Mechanisms of Directed Attention in the Human Extrastriate Cortex as Revealed by Functional MRI. Science (80-.). *282*, 108–111.

Kinsbourne, M. (1977). hemi-neglect and hemisphere rivalry. Adv. Neurol. *18*, 41–49.

Kobayashi, M., Hutchinson, S., Theoret, H., Schlaug, G., and Pascual-Leone, a. (2004). Repetitive TMS of the motor cortex improves ipsilateral sequential simple finger movements. Neurology *62*, 91–98.

Konovalov, A., and Krajbich, I. (2016). Gaze data reveal distinct choice processes underlying model-based and model-free reinforcement learning. Nat. Commun. *7*, 1–11.

Kovach, C.K., Sutterer, M.J., Rushia, S.N., Teriakidis, A., and Jenison, R.L. (2014). Two systems drive attention to rewards. Front. Psychol. *5*.

Krajbich, I., and Rangel, A. (2011). Multialternative drift-diffusion model predicts the relationship between visual fixations and choice in value-based decisions. Proc. Natl. Acad. Sci. U. S. A. *108*, 13852–13857.

Krajbich, I., Armel, C., and Rangel, A. (2010). Visual fixations and the computation and comparison of value in simple choice. Nat. Neurosci. *13*, 1292–1298.

Krajbich, I., Hare, T., Bartling, B., Morishima, Y., and Fehr, E. (2015). A

Common Mechanism Underlying Food Choice and Social Decisions. PLoS Comput. Biol. *11*, 1–24.

Laming, D.R.J. (1968). Information theory of choice-reaction times. Inf. Theory Choicereaction Times.

Lea, A.M., and Ryan, M.J. (2015). Irrationality in mate choice revealed by tungara frogs. Science (80-.). 349, 964–966.

Lefebvre, S., Laloux, P., Peeters, a, Desfontaines, P., Jamart, J., and Vandermeeren, Y. (2012). Dual-tDCS Enhances Online Motor Skill Learning and Long-Term Retention in Chronic Stroke Patients. Front. Hum. Neurosci. *6*, 343.

Louie, K., Khaw, M.W., and Glimcher, P.W. (2013). Normalization is a general neural mechanism for context-dependent decision making. Proc. Natl. Acad. Sci. Unites States Am. 110, 6139–6144.

Lim, S.-L., O'Doherty, J.P., and Rangel, A. (2011). The decision value computations in the vmPFC and striatum use a relative value code that is guided by visual attention. J. Neurosci. *31*, 13214–13223.

Liu, T., Pestilli, F., and Carrasco, M. (2005). Transient attention enhances perceptual performance and fMRI response in human visual cortex. Neuron *45*, 469–477.

Martinez-Trujillo, J.C., and Treue, S. (2002). Attentional Modulation Strength in Cortical Area MT. Neuron *35*, 365–370.

De Martino, B., Kumaran, D., Seymour, B., and Dolan, R.J. (2006). Frames, biases, and rational decision-making in the human brain. Science *313*, 684–687.

De Martino, B., Fleming, S.M., Garrett, N., and Dolan, R.J. (2012). Confidence in value-based choice. Nat. Neurosci. *16*, 105–110.

McGinty, V.B., Rangel, A., and Newsome, W.T. (2016). Orbitofrontal Cortex Value Signals Depend on Fixation Location during Free Viewing. Neuron *90*, 1299–1311.

McNeil, B.J., Pauker, S.G., Sox, H.C., and Tversky, A. (1982). On the Elicitation of Preferences for Alternative Therapies. N. Engl. J. Med. *306*, 1259–1262.

Montagna, B., Pestilli, F., and Carrasco, M. (2009). Attention trades off spatial acuity. Vision Res. *49*, 735–745.

Moore, T., and Armstrong, K.M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. Nature *421*, 370–373.

Moore, T., and Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. J. Neurophysiol. *91*, 152–162.

Moore, T., Armstrong, K.M., and Fallah, M. (2003). Visuomotor Origins of Covert Spatial Attention. Neuron *40*, 671–683.

Mulder, M.J., Wagenmakers, E.-J., Ratcliff, R., Boekel, W., and Forstmann, B.U. (2012). Bias in the Brain: A Diffusion Model Analysis of Prior Probability and Potential Payoff. J. Neurosci. *32*, 2335–2343.

Mulder, M.J., van Maanen, L., and Forstmann, B.U. (2014). Perceptual decision neurosciences - a model-based review. Neuroscience *277*, 872–884.

Von Neumann, J., and Morgenstern, O. (1947). Theory of games and economic behavior.

Nyffeler, T., Cazzoli, D., Wurtz, P., Lüthi, M., von Wartburg, R., Chaves, S., Déruaz, A., Hess, C.W., and Müri, R.M. (2008). Neglect-like visual exploration behaviour after theta burst transcranial magnetic stimulation of the right posterior parietal cortex. Eur. J. Neurosci. *27*, 1809–1813.

O'Connell, R.G., Dockree, P.M., and Kelly, S.P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. Nat. Neurosci. *15*, 1729–1735.

O'Craven, K.M., Rosen, B.R., Kwong, K.K., Treisman, A., and Savoy, R.L. (1997). Voluntary attention modulates fMRI activity in human MT-MST. Neuron *18*, 591–598.

Ongür, D., and Price, J.L. (2000). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. Cereb. Cortex *10*, 206–219.

Padoa-Schioppa, C., and Assad, J.A. (2008). The representation of economic value in the orbitofrontal cortex is invariant for changes of menu. Nat. Neurosci. *11*, 95–102.

Padoa-Schioppa, C., and Assad, J. a (2006). Neurons in the orbitofrontal cortex encode economic value. Nature *441*, 223–226.

Pestilli, F., and Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. Vision Res. *45*, 1867–1875.

Pestilli, F., Viera, G., and Carrasco, M. (2007). How do attention and adaptation affect contrast sensitivity? J. Vis. *7*, 9–9.

Philiastides, M.G., and Ratcliff, R. (2013). Influence of branding on preference-based decision making. Psychol. Sci. *24*, 1208–1215.

Platt, M.L., and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. Nature *400*, 233–238.

Polanía, R., Krajbich, I., Grueschow, M., and Ruff, C.C. (2014). Neural oscillations and synchronization differentially support evidence accumulation in perceptual and value-based decision making. Neuron *82*, 709–720.

Polanía, R., Moisa, M., Opitz, A., Grueschow, M., and Ruff, C.C. (2015). The precision of value-based choices depends causally on fronto-parietal phase coupling. Nat. Commun. *6*, 8090.

Rangel, A., Camerer, C., and Montague, P.R. (2008). A framework for studying the neurobiology of value-based decision making. Nat. Rev. Neurosci. *9*, 545–556.

Ratcliff, R., and McKoon, G. (2008). The diffusion decision model: theory and data for two-choice decision tasks. Neural Comput. *20*, 873–922.

Reynolds, J.H., and Desimone, R. (2003). Interacting roles of attention and visual salience in V4. Neuron *37*, 853–863.

Reynolds, J.H., Pasternak, T., and Desimone, R. (2000). Attention Increases Sensitivity of V4 Neurons. Neuron *26*, 703–714.

Roe, R.M., Busemeyer, J.R., and Townsend, J.T. (2001). Multialternative decision field theory: A dynamic connectionst model of decision making. Psychol. Rev. *108*, 370–392.

Roitman, J., and Shadlen, M. (2002). Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J. Neurosci. *22*, 9475–9489.

Ruff, C.C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J.D., Rees, G., Josephs, O., Deichmann, R., and Driver, J. (2006). Concurrent TMS-fMRI and Psychophysics Reveal Frontal Influences on Human Retinotopic Visual Cortex. Curr. Biol. *16*, 1479–1488.

Saygin, A.P., and Sereno, M.I. (2008). Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. Cereb. Cortex *18*, 2158–2168.

Schonberg, T., Bakkour, A., Hover, A.M., Mumford, J.A., Nagar, L., Perez, J., and Poldrack, R.A. (2014). Changing value through cued approach: an automatic mechanism of behavior change. Nat. Neurosci. *17*, 1–9.

Schouten, J.F., and Bekker, J.A. (1967). Reaction time and accuracy. Acta Psychol. (Amst).

Serences, J.T., Shomstein, S., Leber, A.B., Golay, X., Egeth, H.E., and Yantis, S. (2005). Coordination of Voluntary and Stimulus-Driven Attentional Control in Human Cortex. Psychol. Sci. *16*, 114.

Shadlen, M.N., and Kiani, R. (2013). Decision making as a window on cognition. Neuron *80*, 791–806.

Shafir, S., Waite, T.A., and Smith, B.H. (2002). Context-dependent violations of rational choice in honeybees (Apis mellifera) and gray jays (Perisoreus canadensis). Behav. Ecol. Sociobiol. 51, 180–187.

Shimojo, S., Simion, C., Shimojo, E., and Scheier, C. (2003). Gaze bias both reflects and influences preference. Nat. Neurosci. *6*, 1317–1322.

Silvanto, J., Lavie, N., and Walsh, V. (2006). Stimulation of the human frontal eye fields modulates sensitivity of extrastriate visual cortex. J. Neurophysiol. *96*, 941–945.

Simon, H.A., Quarterly, T., and Feb, N. (1955). A Behavioral Model of Rational Choice. Q. J. Econ. *69*, 99–118.

Sparing, R., Thimm, M., Hesse, M.D., Küst, J., Karbe, H., and Fink, G.R. (2009). Bidirectional alterations of interhemispheric parietal balance by non-invasive cortical stimulation. Brain *132*, 3011–3020.

Squire, R.F., Noudoost, B., Schafer, R.J., and Moore, T. (2013). Prefrontal contributions to visual selective attention. Annu. Rev. Neurosci. *36*, 451–466.

Stewart, N., Hermens, F., and Matthews, W.J. (2016). Eye Movements in Risky Choice. J. Behav. Decis. Mak. *29*, 116–136.

Sugrue, L., Corrado, G., and Newsome, W. (2004). Matching Behavior and the Representation of Value in the Parietal Cortex. Science *304*, 1782–1787.

Tajima, S., Drugowitsch, J., and Pouget, A. (2016). Optimal policy for value-based decision-making. Nat. Commun. *7*, 12400.

Takeuchi, N., Tada, T., Toshima, M., Matsuo, Y., and Ikoma, K. (2009). Repetitive transcranial magnetic stimulation over bilateral hemispheres enhances motor function and training effect of paretic hand in patients after stroke. J. Rehabil. Med. *41*, 1049–1054.

Thompson, K.G., Bichot, N., and Schall, J.D. (1997). Dissociation of visual discrimination from saccade programming in the frontal eye field. J. Neurophysiol. *77*, 1046–1050.

Thompson, K.G., Biscoe, K.L., and Sato, T.R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. J. Neurosci. *25*, 9479–9487.

Towal, R.B., Mormann, M., and Koch, C. (2013). Simultaneous modeling of visual saliency and value computation improves predictions of economic choice. Proc. Natl. Acad. Sci. U. S. A. *110*, E3858-67.

Tsetsos, K., Usher, M., and Chater, N. (2010). Preference reversal in multiattribute choice. Psychol. Rev. *117*, 1275–1293.

Tsetsos, K., Chater, N., and Usher, M. (2012). Salience driven value integration explains decision biases and preference reversal. Proc. Natl. Acad. Sci. U. S. A. *109*, 9659–9664.

Tsetsos, K., Moran, R., Moreland, J., Chater, N., Usher, M., and Summerfield, C. (2016). Economic irrationality is optimal during noisy decision making. Proc. Natl. Acad. Sci. *113*, 3102–3107.

Tversky, A., and Kahneman, D. (1981). The framing of decisions and the psychology of choice. Science (80-.). *211*, 453–458.

Usher, M., and McClelland, J.L. (2001). The time course of perceptual choice: the leaky, competing accumulator model. Psychol. Rev.

Usher, M., and McClelland, J.L. (2004). Loss aversion and inhibition in dynamical models of multialternative choice. Psychol. Rev. *111*, 757–769.

Vaidya, A.R., and Fellows, L.K. (2015). Testing necessary regional frontal contributions to value assessment and fixation-based updating. Nat. Commun. *6*, 10120.

Vickers, D. (1970). Evidence for an accumulator model of psychophysical discrimination. Ergonomics.

Vuilleumier, P. (2013). Mapping the functional neuroanatomy of spatial neglect and human parietal lobe functions: progress and challenges. Ann. N. Y. Acad. Sci. *1296*, 50–74.

Vuilleumier, P., Hester, D., Assal, G., and Regli, F. (1996). Unilateral spatial neglect recovery after sequential strokes. Neurology *46*, 184–189.

Weddell, R. a (2004). Subcortical modulation of spatial attention including evidence that the Sprague effect extends to man. Brain Cogn. *55*, 497–506.

Wickelgren, W.A. (1977). Speed-accuracy tradeoff and information processing dynamics. Acta Psychol. (Amst).

Wright, J., and Krekelberg, B. (2014). Transcranial direct current stimulation over posterior parietal cortex modulates visuospatial localization. J. Vis. *14*, 1–15.

Zhang, J., Bogacz, R., and Holmes, P. (2009). A comparison of bounded diffusion models for choice in time controlled tasks. J. Math. Psychol. *53*, 231–241.

Appendix

Appendix to Study 1

Value comparisons during economic choice are causally linked to inter-hemispheric balance in parietal cortex

Andres Mitsumasu [1], Ian Krajbich [2], Rafael Polania [1], Ernst Fehr [1] and Christian C. Ruff [1]

1. Laboratory for Social and Neural Systems Research, Department of Economics, University of Zurich.
2. Departments of Psychology and Economics, The Ohio State University.

Abstract

In order to choose, a decision-maker has to compare the available options. Prior work on value-based choice suggests that this comparison process involves shifts in attentional focus between the choice options (Krajbich et al., 2010; Krajbich and Rangel, 2011). What remains unknown is whether the neural mechanisms underlying the comparison can be influenced so as to bias choices. We identified the posterior parietal cortex (PPC) as the region most likely to be involved in this process (Platt and Glimcher, 1999; Sugrue et al., 2004; Hare et al., 2011; Hunt et al., 2012; Kahnt et al., 2014; Polanía et al., 2014) and utilized bi-hemispheric transcranial direct current stimulation (tDCS) in order to bias neural excitability towards right or left PPC while human subjects performed a value-based decision task. Compared to sham stimulation, both types of tDCS caused distinct effects on choice behavior, particularly for high-value trials. These effects manifested as either a choice bias towards the left option with left anodal-right cathodal (LA-RC) tDCS or a decrease in response time and choice consistency with left cathodal-right anodal (LC-RA) tDCS. These results are inconsistent with the hypothesis that the tDCS protocol merely affects the direction of spatial attention; they rather concur with the notion that the stimulation affects a dynamic comparison process in which evidence is discounted more strongly for unattended alternatives. Our findings suggest that a specialized neural process discounts unattended options in value-based choice and that this function can be altered by electrical stimulation.

Introduction

Growing evidence suggests that overt visual attention has an important influence on choices when a decision-maker has to choose between different rewards (value-based decisions) (Lim et al., 2011; Towal et al., 2013; Cavanagh et al., 2014; Schonberg et al., 2014; Vaidya and Fellows, 2015). Furthermore, recent investigations have shown that value-based decision can be characterized with an attentional version of a drift-diffusion model (aDDM) (Krajbich et al., 2010; Krajbich and Rangel, 2011). Like other sequential sampling models (Bogacz et al., 2006; Mulder et al., 2014), the aDDM proposes that a choice results from a continuous accumulation of evidence in favor of the options. However, a key distinction of the aDDM is that evidence is temporarily biased in favor of the option under the focus of attention because the other alternative is discounted (see Methods).

Despite behavioral evidence consistent with this modulatory role of attention for value-based decisions (Armel, Beaumel, Rangel 2008; Lim, O'Doherty, Rangel 2011; Towal et al., 2013), the issue of causality remains contentious. It is particularly unclear whether it is possible to manipulate the neural mechanisms underlying this biased comparison process in order to influence choice. To answer this question, we here focused on the posterior parietal cortex (PPC) and tested two competing hypotheses about how stimulation of this brain area may influence value-based choices.

Our first hypothesis was based on numerous findings that the human right PPC is a crucial area for the orienting of visual attention. Lesions of the right human parietal cortex can induce attentional biases towards the right side of the visual scene, and these effects are less frequent and weaker when the left parietal cortex is damaged (Kinsbourne, 1977; Vuilleumier et al., 1996; Corbetta et al., 2005; Vuilleumier, 2013). Moreover, inhibitory transcranial magnetic (TMS) or direct current (tDCS) stimulation over the right PPC can also induce an increased focus towards the right visual field (Hilgetag et al., 2001; Nyffeler et al., 2008; Sparing et al., 2009). Interestingly, compared to unilateral tDCS, this effect is particularly pronounced and appears earlier with bilateral left-anodal/right-cathodal (LA-RC) stimulation (Giglia et al., 2011). Thus, the first hypothesis we tested is that subjects receiving LA-RC tDCS over PPC will have an attentional bias towards options presented on the right side of the display and will therefore be more likely to choose this alternative, relative to a sham group without neurally effective tDCS.

Our second hypothesis was based on decision-making studies suggesting an involvement of the PPC in both the processing of value (Platt and Glimcher, 1999; Sugrue et al., 2004; Hare et al., 2011; Polanía et al., 2014) and the accumulation of evidence underlying choices (Roitman and Shadlen, 2002; Heekeren et al., 2004; Filimon et al., 2013). Together with the aDDM framework, these results suggest that neural processes in parietal cortex could implement the attentional discounting operation that weakens the impact of unattended options on the value comparison process. We therefore tested the hypothesis that tDCS will differentially change the discount of unattended options depending on the electrode montage: A subject under LA-RC stimulation would more strongly discount the unattended option on the right side of the visual field (when focusing on the left alternative) than the unattended left option (when focusing on the right alternative). As a consequence, this subject would accumulate evidence in a biased fashion towards the left option (contrary to the purely attention-based hypothesis outlined in the previous paragraph). Conversely, LC-RA stimulation would lead to a stronger discount of the unattended left option than the unattended right option, thereby biasing the evidence accumulation process towards the right alternative. According to the aDDM, these evidence accumulation biases would particularly affect choices between options with higher overall value because of the multiplicative effect of the attentional discount.

We tested the prediction of both these hypotheses and, as detailed below, our results provide no support for the first hypothesis and are more consistent with the second hypothesis.

Materials and methods

Experimental procedure. Forty human (16 females, mean age +/- SD = 21.3 +/- 1.96) subjects without a history of implanted metal objects, seizures or any other neurological or psychiatric disease participated in the experiment. In a first task, subjects rated 148 food items (average duration of 9 minutes and 57 seconds, SD = 1 minute and 11 seconds). Every food item was presented individually on a computer screen for 2 seconds, followed by a rating screen (free response time). Subjects were instructed to press the space bar for those food items that they did not like at all and to rate the remaining items on a scale from 0 to 10 based on how much they would like to eat that food at the end of the experiment. This rating task gave us a measure of the subjective value for each food item and allowed us to exclude disliked items (Figure 1A). In a second task (average duration of 15 minutes and 15 seconds, SD = 2 minute and 58 seconds), participants made 195 decisions between pairs of positively rated food items. In each trial, one of the food items was presented on the left and the other on the right side of the screen. Decisions were self-paced and were made using the computer keyboard (Figure 1 B). The food items we presented were selected such that – for each participant – the difference in ratings between the left and right items (VD = left item value - right item value) was constrained to be -1, 0 or +1, with an equal number of trials (65) of each. This was done to focus on difficult choice problems where tDCS-induced changes in the decision process would be more likely to change the choice outcomes. Subjects knew that at the end of the experiment, one trial would be selected at random and that they had to eat the food item that they chose in that trial. Subjects were asked not to eat for three hours before the experiment and after the experiment they stayed for thirty minutes in a waiting room where they ate the selected food item. Both tasks were programmed in Matlab 2012b (Matworks), using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007).

Stimulation. Subjects performed the choice task while receiving bi-hemispheric tDCS over the posterior parietal cortex (PPC). This technique consists of applying a constant low electrical current between two electrodes mounted at the scalp in order to reduce (under cathodal electrode) or increase (under anodal electrode) cortical excitability (Nitsche and Paulus, 2000). One group of subjects (n = 14) received left cathodal–right anodal stimulation (LC-RA), a second group (n = 13) received left anodal–right cathodal stimulation (LA-RC), and a third group received Sham stimulation (n = 13). As mentioned above, bilateral tDCS was chosen as it has been shown to induce stronger attention-related effects than unilateral stimulation during visual decision tasks (Sparing et al., 2009; Giglia et al., 2011). Stimulation was delivered with a constant-current stimulator (neuroConn GmbH, Ilmenau, Germany) and a pair of rubber (5 x 5 cm) electrodes. Complying with current safety guidelines (Nitsche et al., 2003; Lyer et al., 2005), a constant current of 1mA intensity was applied. In line with montage used in the investigations mentioned above, the electrodes were placed over P3 and P4 of the international 10–20 system for electroencephalography electrode placement. For all subjects, stimulation started three minutes before the beginning of the choice task. For the non-sham subjects (LA-RC and LC-RA groups), stimulation started with a gradual ramp-up of the current during 30 seconds and it ended once all choices were complete. Subjects in the Sham stimulation group received the same 30 seconds ramping-up stimulation period - which provides a good control by mimicking the skin sensations at the onset of the current without resulting in measurable neural effects (Gandiga et al., 2006) - followed by a 30 seconds period when current gradually ramped-down to zero.

General Setup. The experiment (including both the rating and choice task) was conducted in the computerized group room of the Laboratory for Social and Neural Systems research (SNS-Lab). The group room comprises 14 identical computer workstations that are interconnected and shielded in view from one another. The experiment was conducted in several sessions and each session included multiple subjects (average 12 subjects per session). For each session, subjects were randomly and evenly divided into the three stimulation groups. A multi-channel tDCS system (from NeuroConn, Ilmenau, Germany) was used to simultaneously stimulate each of the participants with either LA-RC, sham, or LC-RA tDCS in each session. This group testing of participants thus controlled for unspecific effects, such as order, experimenter, and time of day effects that may potentially confound serial testing regimes.

Computational model and statistical analysis. The aDDM decomposes the underlying decision-making process as follows: when a subject focuses on the left option, the relative decision value (RDV) progresses according to

$$V_t = V_{t-1} + d(r_{left} - \theta_1 r_{right}) + \xi$$

and when the subject is focused on the right option, the RDV changes according to

$$V_t = V_{t-1} + d(\theta_2 r_{left} - r_{right}) + \xi.$$

V_t is the value of the RDV at time t, d is a constant that controls the speed of change (in units of ms^{-1}), and r_{left} and r_{right} denote the values of the two options. θ_1 and θ_2 (between 0 and 1) are the weights that discount the right or left item when not fixated. In other words, these parameters capture the effect of attentional focus that biases value comparisons. The model implies that the influence of attentional focus on the decision process increases when both options have higher values because of the multiplicative effect of these discount parameters. ξ is white Gaussian noise with variance σ_1^2 or σ_2^2 depending on which item is being fixated (randomly sampled once every millisecond). The upper boundary (UB) corresponds to the left item and the lower boundary (LB) to the right item. In the standard aDDM, $\theta_1 = \theta_2$, UB = LB, and $\sigma_1 = \sigma_2$. However, we examined whether tDCS might break the symmetry and create a lateralized bias in the model.

We tested two competing hypotheses about how tDCS on the PPC would affect the comparison process underlying value-based choices. According to the first hypothesis, LA-RC stimulation (compared to sham tDCS) would lead to a greater likelihood of choosing the right option, due to an increased propensity to orient attentional focus towards that option. The alternative second hypothesis we tested was that bilateral tDCS over the PPC would modulate the contribution of items outside the focus of attention on the evidence-accumulation process, by changing the discounts θ_1 and θ_2 in the aDDM. Whereas the first hypothesis mainly stipulates a main effect of LA-RC stimulation on choice, the second hypothesis implies (1) that both tDCS montages would affect the decision-process in different ways and (2) that these tDCS modulations would affect choice behavior more strongly on trials with higher OV because of the multiplicative effect of the discounts.

To examine this hypothesis, we used the aDDM to identify the simplest possible changes in the value comparison process that could account for the observed pattern of behavioral results. In other words, we examined which stimulation-induced parameter changes in the aDDM can account for the pattern of observed choices and response times across stimulation groups. To test how the effects of the different tDCS montages could best be explained, we simulated different models and compared their predictions with the empirical results (see Table 1). This set of models (Models 1-3) formalized how tDCS may have modulated the influence of attentional focus on evidence accumulation by changing the parameters θ_1 and θ_2. According to Model 1, the discounting of the right unattended option is stronger (θ_1 becomes smaller) under LA-RC stimulation relative to Sham stimulation, whereas LC-RA stimulation increases the discounting of the left unattended alternative (θ_2 becomes smaller). Model 2 implies that LA-RC stimulation decreases the discount of the left unattended alternative (θ_2 becomes higher), whereas LC-RA stimulation decreases the discount of the right unattended option (θ_1 becomes higher). Model 3 assumes that the discounting of both options increases with LA-RC, and decreases with LC-RA stimulation. We additionally simulated an analogous set of models (Models 4-6) formalizing that tDCS may have injected or reduced noise in the decision process, by changing the parameters σ_1 and σ_2. Finally, a third set of models (Models 7-9) was based on the assumption that stimulation may have modified the amount of net accumulated evidence required to implement a choice, by changing UB and LB. For simplicity, these three sets of models only considered symmetrical effects of the two tDCS treatments on the values of the θ, σ, or the choice barrier (UB, LB) parameters.

We used the R package for statistical analysis of the behavioral results from the decision task (lme4 extension) and to perform the model simulations. Each trial from the Sham group was simulated with the parameters obtained in previous investigations with healthy non-stimulated subjects (Krajbich et al., 2010; Krajbich and Rangel, 2011). Note that, unlike these previous investigations, our aDDM does not impose a single discount factor for the unattended option but allows for different discount factors for an unattended right (θ_1) or left (θ_2) food item (Table 1). Each trial in the binary choice task was simulated 100 times with each model. Each trial simulation started with a higher probability of an initial fixation towards the left food image (p=0.74, as reported in Krajbich et al., 2010) and fixations alternated between the left and right food images until the RDV reached a choice barrier. To simulate the pattern of shifts in attentional focus, we used the distribution of fixation durations observed in a similar food-choice experiment (Krajbich et al., 2010).

In line with the simulation procedure from that previous experiment, the periods of attentional focus were sampled randomly from the empirical distribution of non-last fixations, conditional on whether the fixation was the first or non-first of the trial. To examine the effects of different parameterizations of the aDDM, we performed logistic regressions with choices as the dependent variable and value differences (VD), overall values (OV) and interactions with stimulation group dummies as independent variables; the data from the sham group served as baseline in this regressions. Additionally, we performed linear regressions on reaction times as the dependent variable. These linear regressions were similar except that we used the absolute value difference (|VD|) as an independent variable, instead of the VD.

Results

Decision behavior

Our first hypothesis implies that LA-RC stimulation increases subjects' propensity to focus on the right side of the screen, thereby generally increasing the probability of choosing the option on the right side. Whereas this hypothesis mainly implies a main effect of LA-RC, our second hypothesis stipulates that both tDCS montages will differentially modulate the contribution of items outside the focus of attention during the decision process. Moreover, whereas our first hypothesis does not involve predictions on OV, our second hypothesis implies that higher OV leads to both larger effects of attentional focus on choice and shorter response times (RTs) (see Materials and Methods for more details). To test these two alternative hypotheses, we analyzed possible stimulation effects on subjects' choices. We ran a mixed-effects regression of choices as the dependent variable on value difference (VD = left item value – right item value), OV and stimulation group dummies as independent variables. We also included interactions of OV and VD with the stimulation group dummies and random effects to account for repeated within-subject measures (See supplementary table 1).

Subjects in all three groups were more likely to choose the higher-valued food item as the VD between the two items increased ($p < 10^{-10}$), confirming that subjects were consistent with their earlier ratings. Relative to the baseline sham group, there was no main effect for any active tDCS montage (LA-RC: $p = 0.10$; LC-RA: $p = 0.62$). However, compared to the sham group, subjects receiving LA-RC stimulation were more likely to choose the left item as the OV increased (LA-RC x OV: $p = 0.029$) (Figure 1C Bottom Left). Note that this choice bias towards the left alternative is opposite to the one expected under our first hypothesis, and depends on OV as expected under our second hypothesis.

To test the predictions of the aDDM on RTs, we ran an analogous linear mixed-effects regression on RTs (Supplementary table 2). There was no main effect of any stimulation group or |VD| (LA-RC: $p = 0.41$; LC-RA: $p = 0.17$; |VD|: $p = 0.33$), nor any interaction effects between stimulation groups and |VD| (LA-RC x |VD|: $p = 0.24$; LC-RA x |VD|: $p= 0.28$). However, consistent with our second hypothesis, this analysis confirmed that subjects chose faster in trials with higher OV ($p < 0.014$); this effect was stronger for subjects receiving LC-RA stimulation (LC-RA x OV: $p = 0.005$) but not for subjects in the LA-RC group (LA-RC x OV: $p = 0.16$) (Figure 1C Top).

Finally, we ran a third mixed-effects logistic regression to further identify any effects of tDCS on choice consistency (i.e., the likelihood of choosing the item with the higher rating). We only included choices between unequally rated items ($VD \neq 0$) in this analysis. This analysis revealed a negative effect of LC-RA stimulation ($p < 0.047$), meaning that subjects with LC-RA stimulation made choices that were less consistent with their earlier ratings than subjects in the baseline Sham group (Figure 1C Bottom right). This effect was not observed with LA-RC stimulation ($p = 0.95$) (Supplementary table 3).

Computational model simulations

The behavioral results observed in our experiment are inconsistent with the first hypothesis because we do not observe a choice bias towards the right item in the LA-RC group. Can our second hypothesis – which stipulates that our two tDCS treatments induce changes in the discount factors θ_1 and θ_2 for the unattended options – provide a unifying explanation of all the behavioral regularities described above? To answer this question, we tested three different models (Models 1-3) that simulated symmetric tDCS-induced changes in the values of the discounts θ. Additionally, we simulated analogous models in order to examine whether these behavioral patterns were induced by modulations of other aspects of the decision process, such as the noise (Models 4-6) or the net evidence required to implement the decisions (i.e. the upper and lower boundaries, Models 7-9). Only one of the simulated aDDMs replicated the effects on choice, RTs and accuracy (Table 1). This model is based on the idea that LA-RC and LC-RA stimulation produce symmetric changes in the discount parameters θ_1 and θ_2. More precisely, the model assumes that LA-RC stimulation increases the discounting of an unattended right item (decrease in θ_1) whereas LC-RA has a symmetric effect of increasing the discounting of an unattended left item (decrease in θ_2) (Figure 2 D and E). In line with the data, this model produces choice biases that are amplified as OV increases (Figure 2 B and C).

One might wonder how a symmetric bias in attentional discounting produces an asymmetric bias in the choice behavior. We believe that the key towards understanding this is that subjects show a robust tendency to start exploration with an initial gaze towards the left side of the visual scene (Butler et al., 2005; Dickinson and Intraub, 2009; Foulsham et al., 2013; Ossandón et al., 2014), leading to an initial bias in the accumulation of evidence towards the left option (Krajbich et al., 2010). This initial tendency to focus on the left item, coupled with the extra discount on the right item from the LA-RC stimulation, leads to more choices of the left item. On the other hand, although LC-RA stimulation causes an extra discount of the unattended left item, this bias against choosing left is counteracted by the subjects' strong general tendency to focus on the left item first. In other words, with LC-RA stimulation, the initial phase of evidence accumulation is not strongly supporting one alternative over the other, and the decision process is determined by the subsequent shifts of focus, leading to more-error prone choices.

Discussion

The aim of this experiment was to evaluate how modulations of neural activity in the PPC influenced the comparison process underlying value-based decisions. To do so, we examined two competing hypotheses on how bilateral tDCS on the PPC may influence this process. The first of these hypotheses was derived from previous studies of tDCS effects on visual attention and predicted that LA-RC stimulation would lead to an increased tendency to choose the option presented on the right side of the visual scene. The second hypothesis was based on the decision process described by the aDDM and implied that LA-RC and LC-RA stimulation would modulate the contribution of alternatives out of focus on evidence accumulation.

The results of our experiment showed a complex pattern of choice behavior that could not be explained by our first hypothesis. As predicted by the aDDM, decisions with higher OV led to faster responses in our three groups of subjects, and this effect increased with LC-RA stimulation. Additionally, LA-RC stimulation increased the likelihood of choosing the left option, but mainly in decisions with high OV. Finally, LC-RA stimulation led to a decrease in choice consistency.

On the basis of aDDM simulations, we were able to rationalize these regularities with a simple symmetric modulation of the discount parameter θ and provide evidence in favor of our second hypothesis. Our modeling results indicate that bilateral tDCS of the PPC was most likely to decrease evidence accumulation for unattended items ipsilateral to cathodal stimulation and contralateral to anodal stimulation. In other words, these results suggest that our bilateral montage of LA-RC (LC-RA) increases the discount in the evidence accumulation process for an unattended right (left) option but has no effect on the discount factor for an unattended left (right) option.

This explanation suggests that the effects induced by tDCS impacted on the value computation and/or comparison process rather than on spatial attention per se, since the observed choice biases are opposite to what would be predicted by reported effects of our tDCS montage on the distribution of spatial attention in simple visual tasks. For instance, recent investigations using simple perceptual judgments have shown that cathodal tDCS over the right PPC induces a rightward bias and that this effect is greater with bi-hemispheric LA-RC stimulation (Sparing et al., 2009; Giglia et al., 2011). It is important to emphasize that our results do not contradict these data. Those studies involved perceptual judgments (e.g., bisection of horizontal lines) in order to measure subtle changes in the allocation of spatial attention, while our study involved lengthy comparisons between value representations of highly salient food images. These high-resolution images are powerful visual stimuli and unlikely to be neglected as a result of tDCS. Furthermore, please note that the observed behavioral effects are also unlikely to be due to other task-general factors such as motor biases, since they were systematically amplified in decisions involving high OV, as predicted by the aDDM (Figure 2 C).

It is important to note that the space of models that we tested was by no means exhaustive. Our goal was to find the most parsimonious explanation for the observed behavioral effects. It may be the case that other more complicated explanations could also provide an explanation for the observed regularities. However, even with the restriction to symmetric effects on the discount parameters, we were able to provide a unifying explanation of the observed behavioral regularities.

An important question raised by our results is how tDCS affects interconnected areas within the same hemisphere during value-based decisions. Recent work suggests that synchronized fronto-parietal activity is a neural fingerprint of value-based choices (Hunt et al., 2012; Polanía et al., 2014, Siegel et al. 2008) and it is possible that the effects of our tDCS montage involve reduced sensitivity of parietal areas for signals originating in frontal cortex (Polania et al, 2015). Another important question concerns the specific contributions of anodal and cathodal stimulation in these behavioral patterns, which is generally unclear for the standard montage we employed here based on previous work (Sparing et al., 2009; Giglia et al., 2011). Theories of inter-hemispheric competition emphasize the role of mutually inhibitory connections between homologous brain areas across hemispheres (parietal, frontal and collicular regions) (Sprague, 1966; Kinsbourne, 1977; Kapur, 1996). According to this view, mutual inhibition leads to an adequate distribution of neural activity between hemispheres. Several investigations suggest that causal manipulations of neural activity in these areas lead to asymmetric inter-hemispheric interaction and, therefore, biases in motor and perceptual functions (Funk and Pettigrew, 2003; Kobayashi et al., 2004; Weddell, 2004; Hummel and Cohen, 2006; Sparing et al., 2009; Takeuchi et al., 2009; Giglia et al., 2011; Lefebvre et al., 2012; Wright and Krekelberg, 2014; Filmer et al., 2015). Our study provides suggestive evidence for the role of these inter-hemispheric dynamics in value-based choice and motivates further research into the precise underlying mechanisms.

To summarize, we combined tDCS and computational modeling techniques to demonstrate that value-based choices can be manipulated by stimulating PPC. Our results support the idea that bilateral tDCS over the PPC causes a symmetric spatial bias in the accumulation of value information, resulting in biased choices.

References

Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD (2006) The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. Psychol Rev 113:700–765.

Cavanagh JF, Wiecki T V, Kochar A, Frank MJ (2014) Eye tracking and pupillometry are indicators of dissociable latent decision processes. J Exp Psychol Gen 143:1476–1488.

Corbetta M, Kincade MJ, Lewis C, Snyder AZ, Sapir A (2005) Neural basis and recovery of spatial attention deficits in spatial neglect. Nat Neurosci 8:1603–1610.

Filimon F, Philiastides MG, Nelson JD, Kloosterman N a, Heekeren HR (2013) How embodied is perceptual decision making? Evidence for separate processing of perceptual and motor decisions. J Neurosci 33:2121–2136.

Filmer HL, Dux PE, Mattingley JB (2015) Dissociable effects of anodal and cathodal tDCS reveal distinct functional roles for right parietal cortex in the detection of single and competing stimuli. Neuropsychologia:1–7.

Funk AP, Pettigrew JD (2003) Does interhemispheric competition mediate motion-induced blindness? A transcranial magnetic stimulation study. Perception 32:1325–1338.

Giglia G, Mattaliano P, Puma a, Rizzo S, Fierro B, Brighina F (2011) Neglect-like effects induced by tDCS modulation of posterior parietal cortices in healthy subjects. Brain Stimul 4:294–299.

Heekeren HR, Marrett S, Bandettini P a, Ungerleider LG (2004) A general mechanism for perceptual decision-making in the human brain. Nature 431:859–862.

Hilgetag CC, Théoret H, Pascual-Leone a (2001) Enhanced visual spatial attention ipsilateral to rTMS-induced “virtual lesions” of human parietal cortex. Nat Neurosci 4:953–957.

Hummel FC, Cohen LG (2006) Non-invasive brain stimulation: a new strategy to improve neurorehabilitation after stroke? Lancet Neurol 5:708–712.

Hunt LT, Kolling N, Soltani A, Woolrich MW, Rushworth MFS, Behrens TEJ (2012) Mechanisms underlying cortical activity during value-guided choice. Nat Neurosci 15:470–476, S1-3.

Kapur N (1996) Paradoxical functional facilitation in brain-behaviour research. Brain 119:1775–1790.

Kinsbourne M (1977) hemi-neglect and hemisphere rivalry. Adv Neurol 18:41–49.

Kobayashi M, Hutchinson S, Theoret H, Schlaug G, Pascual-Leone a. (2004) Repetitive TMS of the motor cortex improves ipsilateral sequential simple finger movements. Neurology 62:91–98.

Krajbich I, Armel C, Rangel A (2010) Visual fixations and the computation and comparison of value in simple choice. Nat Neurosci 13:1292–1298.

Krajbich I, Rangel A (2011) Multialternative drift-diffusion model predicts the relationship between visual fixations and choice in value-based decisions. Proc Natl Acad Sci U S A 108:13852–13857.

Lefebvre S, Laloux P, Peeters a, Desfontaines P, Jamart J, Vandermeeren Y (2012) Dual-tDCS Enhances Online Motor Skill Learning and Long-Term Retention in Chronic Stroke Patients. Front Hum Neurosci 6:343.

Lim S-L, O’Doherty JP, Rangel A (2011) The decision value computations in the vmPFC and striatum use a relative value code that is guided by visual attention. J Neurosci 31:13214–13223.

Mulder MJ, van Maanen L, Forstmann BU (2014) Perceptual decision neurosciences - a model-based review. Neuroscience 277:872–884.

Nyffeler T, Cazzoli D, Wurtz P, Lüthi M, von Wartburg R, Chaves S, Déruaz A, Hess CW, Müri RM (2008) Neglect-like visual exploration behaviour after theta burst transcranial magnetic stimulation of the right posterior parietal cortex. Eur J Neurosci 27:1809–1813.

Polanía R, Krajbich I, Grueschow M, Ruff CC (2014) Neural oscillations and synchronization differentially support evidence accumulation in perceptual and value-based decision making. Neuron 82:709–720.

Roitman J, Shadlen M (2002) Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J Neurosci 22:9475–9489.

Schonberg T, Bakkour A, Hover AM, Mumford JA, Nagar L, Perez J, Poldrack RA (2014) Changing value through cued approach: an automatic mechanism of behavior change. Nat Neurosci 17:1–9.

Shimojo S, Simion C, Shimojo E, Scheier C (2003) Gaze bias both reflects and influences preference. Nat Neurosci 6:1317–1322.

Sparing R, Thimm M, Hesse MD, Küst J, Karbe H, Fink GR (2009) Bidirectional alterations of interhemispheric parietal balance by non-invasive cortical stimulation. Brain 132:3011–3020.

Sprague JM (1966) Interaction of cortex and superior colliculus in mediation of visually guided behavior in the cat. Science 153:1544–1547.

Takeuchi N, Tada T, Toshima M, Matsuo Y, Ikoma K (2009) Repetitive transcranial magnetic stimulation over bilateral hemispheres enhances motor function and training effect of paretic hand in patients after stroke. J Rehabil Med 41:1049–1054.

Towal RB, Mormann M, Koch C (2013) Simultaneous modeling of visual saliency and value computation improves predictions of economic choice. Proc Natl Acad Sci U S A 110:E3858-67.

Vaidya AR, Fellows LK (2015) Testing necessary regional frontal contributions to value assessment and fixation-based updating. Nat Commun 6:10120.

Vuilleumier P (2013) Mapping the functional neuroanatomy of spatial neglect and human parietal lobe functions: progress and challenges. Ann N Y Acad Sci 1296:50–74.

Vuilleumier P, Hester D, Assal G, Regli F (1996) Unilateral spatial neglect recovery after sequential strokes. Neurology 46:184–189.

Weddell R a (2004) Subcortical modulation of spatial attention including evidence that the Sprague effect extends to man. Brain Cogn 55:497–506.

Wright J, Krekelberg B (2014) Transcranial direct current stimulation over posterior parietal cortex modulates visuospatial localization. J Vis 14:1–15.

Figures

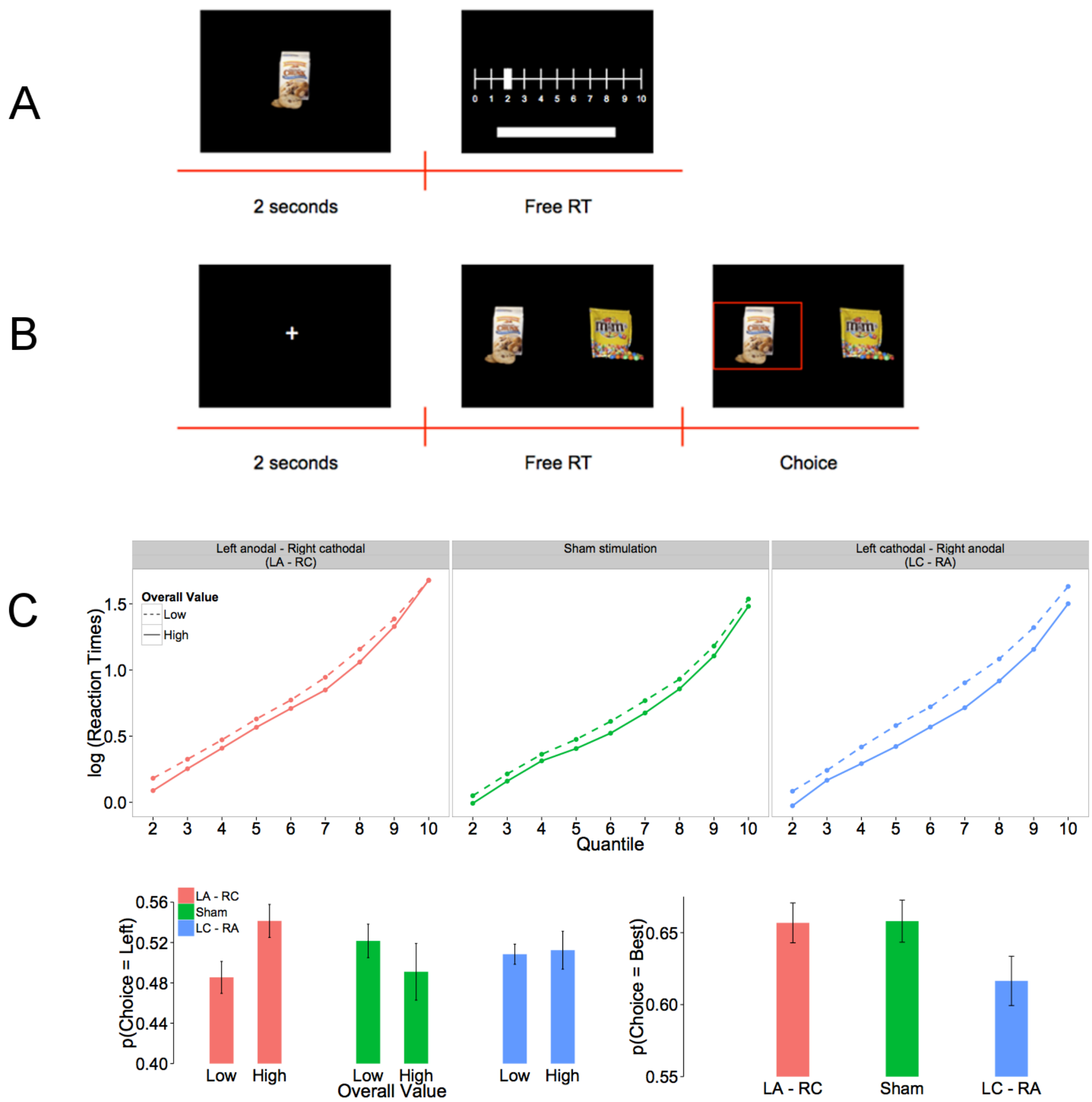

Figure 1. Experiment. (**A**) Rating task. Subjects rated a series of food items from 0 to 10. Disliked items were excluded by pressing the space bar of the computer keyboard (represented by the white rectangle at the bottom of the rating screen). (**B**) Choice task. Subjects were asked to fixate the center cross for 2 seconds. Then two images of food items were presented on the left and the right side of the screen, respectively, and subjects selected (without a time limit) the item they wanted to consume later, at the end of the experiment. After the decision was made, a red box highlighted the selected item. (**C**) Behavior conditional on stimulation group and overall value (low vs. high). Top: Reaction times (RTs) binned in quantiles. For visualization purposes, the first and last quantile are not shown. Bottom Left: Probability of choosing the left item as a function of overall value and tDCS group. Bottom Right: Probability of choosing the best item as function of tDCS group.

A

$$\text{Sham:}\quad V_t = \begin{cases} V_{t-1} + d\,(r_{left} - \theta_1 r_{right}) + \varepsilon & \text{if left item fixated} \\ V_{t-1} + d\,(\theta_2 r_{left} - r_{right}) + \varepsilon & \text{if right item fixated} \end{cases}$$

$$\text{LA-RC:}\quad V_t = \begin{cases} V_{t-1} + d\,(r_{left} - \theta'_1 r_{right}) + \varepsilon \\ V_{t-1} + d\,(\theta_2 r_{left} - r_{right}) + \varepsilon \end{cases} \qquad \theta'_1 < \theta_1$$

$$\text{LC-RA:}\quad V_t = \begin{cases} V_{t-1} + d\,(r_{left} - \theta_1 r_{right}) + \varepsilon \\ V_{t-1} + d\,(\theta'_2 r_{left} - r_{right}) + \varepsilon \end{cases} \qquad \theta'_2 < \theta_2$$

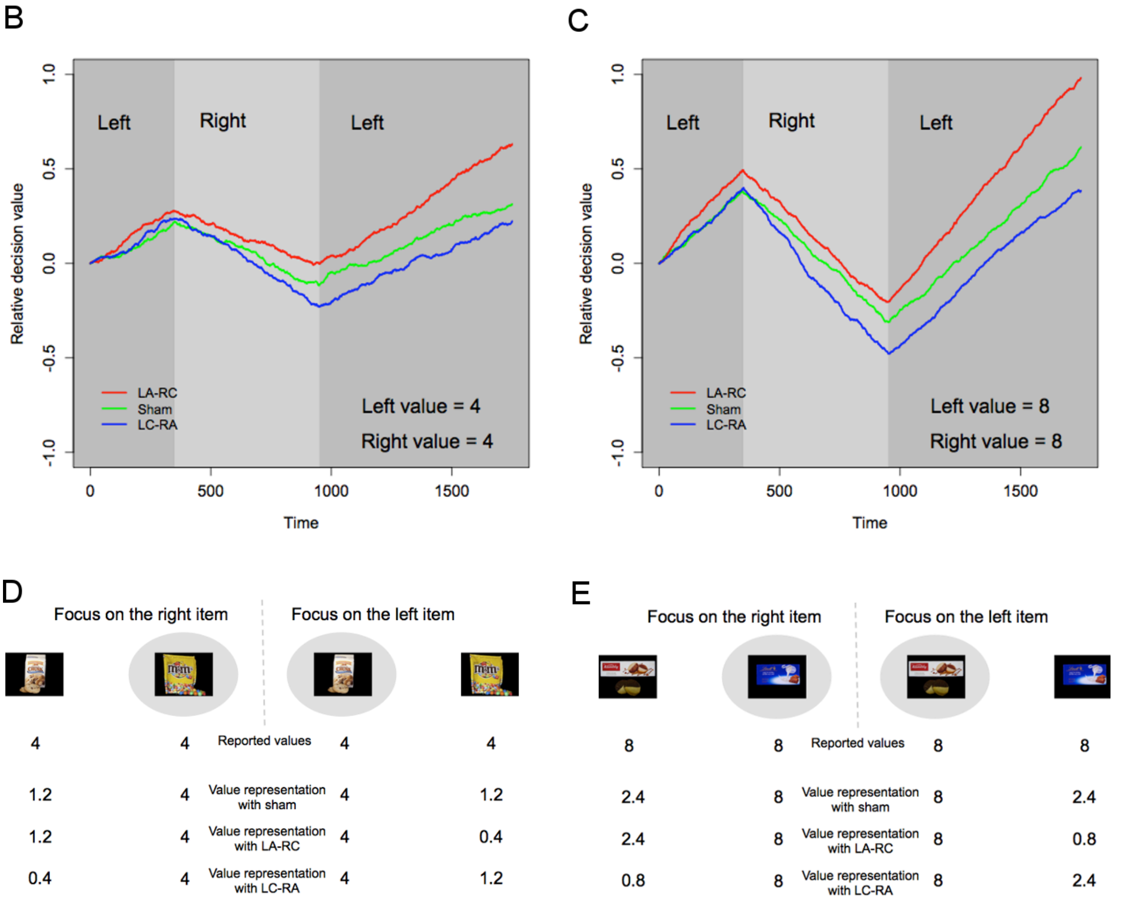

Figure 2. Computational modeling framework. (**A**) The best model increases the discounting of the right unattended (lowers θ_1 : $\theta'_1 < \theta_1$) option under LA-RC stimulation, while under the LC-RA stimulation, it increases the discounting of the left unattended alternative (lowers θ_2 : $\theta'_2 < \theta_2$). (**B**) This model implies that the RDV progresses in favor of the attended item. LA-RC stimulation biases the RDV towards the upper boundary (left item) while LC-RA stimulation biases the RDV towards the lower boundary. (**C**) The RDV progresses faster in decisions with high overall value, leading to faster choices and stronger modulations of tDCS in choice. (**D**) Example of the tDCS effects on value comparisons in to our model when both items have a rating value of 4. The gray area signals the focused item. Our model implies that the item out of focus has a disadvantage relative to the item in focus because only a fraction of its value is computed during the comparison process. LA-RC stimulation further increases the disadvantage of the item in the right visual periphery, while the disadvantage of the item in the left visual periphery is increased with LC-RA stimulation. (**E**) In decisions with high OV, the disadvantage of items out of focus and the effects of tDCS are stronger.

Model	Parameter modified	Group			Effect				
					Choice bias		RTs		Accuracy
		Sham	LA-RC	LC-RA	VD	LA-RC * OV	OV	LC-RA * OV	LC-RA
Model 1	θ_1	0.3	0.1	0.3	✔	✔	✔	✔	✔
	θ_2	0.3	0.3	0.1					
Model 2	θ_1	0.3	0.3	0.5	✔	✔	✔		
	θ_2	0.3	0.5	0.3					
Model 3	θ_1	0.3	0.1	0.5	✔	✔	✔		
	θ_2	0.3	0.1	0.5					
Model 4	σ_1	0.02	0.005	0.02	✔	✔	✔	✔	
	σ_2	0.02	0.02	0.005					
Model 5	σ_1	0.02	0.02	0.04	✔	✔	✔		✔
	σ_2	0.02	0.04	0.02					
Model 6	σ_1	0.02	0.01	0.03	✔		✔		✔
	σ_2	0.02	0.01	0.03					
Model 7	UB	1	0.7	1	✔		✔		✔
	LB	1	-1	-0.7					
Model 8	UB	1	1	1.3	✔		✔		
	LB	1	-1.3	-1					
Model 9	UB	1	0.7	1.3	✔		✔		
	LB	1	-1.3	-0.7					

Table 1. Models used to simulate the choices in the decision task. Parameter values to simulate the decisions corresponding to the Sham group were taken from Krajbich et al., 2010. Only Model 1 reproduced all the effects of Left anodal – Right cathodal (LA-RC) and Left cathodal – Right anodal (LC-RC) stimulation (as indicated by the symbol ✔ in each column). UB and LB denote Upper Boundary and Lower Boundary. VD denotes the difference between the rating values of the left and the right item. Ov denotes overall value.

Supplementary material

	Coefficient	Standard Error	Z value	P value
Intercept	0.11	0.08	1.42	0.15
LA-RC	-0.20	0.12	-1.64	0.10
RA-LC	-0.06	0.12	-0.50	0.62
VD	0.64	0.10	6.67	$2.63e^{-11}$
OV	-0.01	0.01	-1.23	0.22
LA-RC x VD	-0.09	0.15	-0.61	0.54
LA-RC x OV	0.03	0.01	2.18	0.029
LC-RA x VD	-0.21	0.14	-1.46	0.14
LC-RA x OV	0.01	0.01	0.53	0.59
VD x OV	0.00	0.01	0.20	0.84
LA-RC x VD x OV	0.01	0.01	0.53	0.59
LC-RA x VD x OV	0.00	0.02	0.21	0.84

Supplementary table 1

Logistic mixed-effects regressions on the probability of choosing left option. Dependent variable equals 1 if the safe option is chosen and 0 otherwise. Subject identity was used as a random effect to account for repeated measures.

	Coefficient	Standard Error	Z value	P value
Intercept	0.75	0.09	8.54	$2e^{-16}$
LA-RC	0.10	0.13	0.81	0.42
RA-LC	0.17	0.12	1.36	0.17
|VD|	-0.04	0.04	-0.96	0.34
OV	-0.01	0.00	-2.47	0.013
LA-RC x |VD|	0.07	0.06	1.17	0.24
LA-RC x OV	0.01	0.00	1.40	0.16
LC-RA x |VD|	0.06	0.06	1.08	0.28
LC-RA x OV	-0.01	0.01	-2.81	0.005
|VD| x OV	0.00	0.00	1.02	0.31
LA-RC x |VD| x OV	-0.01	0.01	-1.45	0.15
RA-LC x |VD| x OV	-0.01	0.01	-0.87	0.38

Supplementary table 2

Linear mixed-effects regression on reaction times (RTs). The dependent variable is the log of the RTs (which were measured in milliseconds). This log transform was performed to account for the skewed distribution of the RTs. Subject identity was used as a random effect to account for repeated measures.

	Coefficient	Standard Error	Z value	P value
Intercept	0.66	0.07	10.00	$<2e^{-16}$
LA-RC	-0.01	0.09	-0.06	0.95
RA-LC	-0.18	0.09	-1.99	0.047
|VD|	-0.01	0.05	-0.21	0.84
LA-RC x |VD|	0.03	0.07	0.44	0.66
LC-RA x |VD|	0.04	0.07	0.61	0.54

Supplementary table 3

Logistic mixed-effects regressions on the probability of choosing best option. Dependent variable equals 1 if the best option is chosen and 0 otherwise. Subject identity was used as a random effect to account for repeated measures. For this regression, only trials with an absolute value difference (|VD|) different from 0 were included.